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DECEMBER 30, 1933

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CONDITIONS OF LIFE IN THE OCEAN

By AUGUST KROGH

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I owe you an apology for coming forward to speak to you about the conditions of life in the ocean. You have the right to expect that the speakers on this grand occasion are experts in their fields and have made material contributions to the progress of the century in the chosen field. I am certainly no expert on oceanic life. Although I have been interested in it from early youth, circumstances have directed my work into other channels and it is only in quite recent years that I have been actively engaged in studies connected with the problems of life in the ocean. I approach these problems now from the point of view of a physiologist with all the bias and I hope with some of the experience which that involves, and I shall speak to you about them as a physiologist specially interested in the energetics of life.

The energetic processes on which life depends are essentially the same in the sea as on land, but the conditions differ so much that this essential similarity can hardly be recognized.

In the sea as on land the substances making up the organisms and constituting the food for animals are built up by plants utilizing the energy of the sun's rays, while all organisms break down the complex substances and liberate the energy which is partially turned to use in their manifestations of life.

In the sea animal life is distributed over the whole range of depth which reaches for the Atlantic Ocean a mean of nearly 4000m, while the absence of light in deeper strata restricts the plant life to the upper layers of 200 or at most 400m. On land the processes of life are in the main concentrated into a space along the surface which is comparatively very shallow. The aspect of life on land being so diverse let us take as the basis of our comparison a beech forest which has the advantage that it is only comparatively slightly influenced by the activities of man. To bring out clearly both the similarity and the difference between the manifestations of life in such a forest and in the ocean I must go into some figures.

Disregarding the quantitatively insignificant ground flora beneath the trees the plant life is represented by about 300 individual trees per hectare (120 per acre) representing some 30kg of dry substance per m^2. The average height is about 30m, but only the upper 10m bear leaves carrying on the assimilation. The roots spread to a depth of less than one meter, so that the whole zone of life is only slightly over 30m thick as against the 4000m of the ocean. The annual production of organic dry substance is 1.5kg per sq.m. of which about a fourth is lost again by the respiration of the trees. Of the

surplus about two-thirds go to increase the mass of wood while one-third fall down as leaves. The higher and, so to speak, visible animal life which such a forest supports is quantitatively insignificant, but not so the fauna of the soil which feeds on the dead leaves. Studies recently made in Denmark by Bornebusch have shown the existence in the upper 25cm of forest soil of an enormous number of animals. Taking into account only the forms visible to the naked eye there are from 3,000 to 20,000 animals per m^2 or from 100,000 to over half a million for each tree. Unknown numbers of microscopic animals and bacteria assist these "larger" animals in breaking down the organic substance of the leaves. In the best soil we have the smaller number; earthworms predominate and the total weight can be 80g per sq.m. In poor localities small arthropods predominate and the 20,000 animals weigh only some 15g. To show you the significance of these figures I may mention that the 80g per m^2 compares not unfavourably with the weight of cattle on farmland, and the maximum observed of 200g earthworms per m^2 is about the weight of the total live stock on the best Danish farms.

Turning now to the ocean the figures are less precise, but the differences come out clearly. Below each m^2 of surface and down to a depth of 200m there are an enormous number of microscopic plants associated with a much smaller number which are just visible to the naked eye and a still smaller number of animals from microscopic size upwards.

Under one m^2 near the equator we find down to a depth of 200m something like a billion (10^9) nannoplankton plants with perhaps 4 million just visible phytoplankton organisms and a million animals of various sizes, but mostly microscopic or just visible. The total mass of these myriads of organisms is surprisingly small. By calculations which are somewhat uncertain and likely to rather overestimate the amount I arrive at the figure 30g organic dry substance per m^2 from the surface to 200m or only 0.1% of the corresponding amount in the forest. From the energetic point of view this comparison is misleading, because the trees in the forest stand for a hundred years or more while the plankton renews itself several times a year, but even assuming an average period of life of only 0.1 year the production falls far short of that of the forest being then 300g against 1500g. At high latitudes the quantity of plankton present in spring and summer can be ten or more times higher than the figures just given and the production, although probably still falling short of that that in the forest, is at least of a similar order of magnitude.

What are the reasons for these differences between land and ocean and between different parts of the ocean?

It is clear that in the ocean we could not have large plants. The often violent movements of the water would tear them to pieces, but why should they be microscopically small? There is, I believe, more than one reason for

this, but in the main it is an adaptation to floating. The tissues of organisms are on the whole heavier than water and the silica skeletons of the diatoms for instance are a good deal heavier. The rate of sinking for a body heavier than water depends upon the ratio of surplus weight to friction which in its turn is determined mainly by the surface area. There are a large number of beautiful adaptations to obtain a slow rate of sinking. Time will not permit me to go into them, and I shall only state that the simplest way to obtain a relatively large surface is by reduction in absolute size. The rate of sinking of the minute plankton organisms is so slow that they can remain in the upper strata of the water for the length of their natural lives.

The quantitative poverty of the plankton in the warm water of lower latitudes compared with the cold water of arctic and antarctic seas for a long time puzzled investigators, until Brandt showed that it was due to the very low concentration in the water of some of the necessary constituents of organisms.

Sea water is a solution of a large number of substances. A few of these are present in high or fairly high concentration, while of the majority only traces can be demonstrated by refined chemical methods, and among these are some of the most important plant foods like phosphate and the nitrogen compounds, nitrate, nitrite and ammonia. The concentration of these compounds in sea water is always low compared with the corresponding concentration in ordinary soil. Brandt gives as an example that in good farmland the available nitrogen under 1 sq.m. down to 25cm depth is about 400g, while in the North Sea there are only about 40g in the upper 100m. The concentration per cubic meter is 4,000 times higher in the soil than in the water. The corresponding figures for phosphoric acid is 210g in 25cm thickness of soil per m^2 and 13g in 100m depth of water per m^2—an even greater discrepancy in favour of the soil. To a certain extent this discrepancy is compensated by the movements of the water and the much better conditions for diffusion of the substances, but in all areas where the same water remains at the surface over a long period the nitrogen compounds and phosphates and sometimes also the silica become depleted so as to interfere very seriously with the growth of plants, and this is due to the fact that the organisms in spite of their floating power will gradually sink down and become dissolved below the depth of 200m which is the average lower limit for assimilation.

The problem regarding the supply and regeneration of nitrogen is complicated by interchange with the atmosphere, but the phosphate and silica are simply dissolved out of the dead organisms and go back into solution. The result is that the plant nutrients become accumulated in the deeper strata where they cannot be utilized, while the surface is depleted. If no mixing took place the depletion would go on to exhaustion and life would die out except along the coasts, but in certain areas mainly at fairly high latitudes, but

also for instance in the huge Gulf of Guinea, waters from the deep rise to the surface and become the seat of a large outburst of planktonic life which imparts a distinct tint of green to the water. From these areas of fertility and abundance the waters spread by the currents become progressively poorer in the salts necessary for plant growth and the large areas of the ocean where the water is of a pure blue can only be compared to deserts supporting a minimum of life.

As I said before even in the areas of abundance the concentration of nutrient salts is low in comparison with that of fertile soil and we can find here one more reason for the minuteness of the floating plants. It enables them to obtain their nutriment from very dilute solutions. I shall illustrate this point by means of an example. Suppose we have sea water with a content of available nitrogen in the form of nitrate of 100mg per m^3 and plankton plants growing to $1mm^3$ each requiring only 0.1% of nitrogen. This would mean that each individual plant would have to absorb during its growth all the nitrate from 10cc of the water. This would not be possible, for two reasons. Such absorption takes place through the cell surface and is due to a difference in concentration which can be kept up because the nitrate entering the cell is used for synthesis of substances which are indiffusible. The maximum possible concentration difference in this case is 10^{-7}g per cm^3 outside and 0.0 inside, when namely the nitrate concentration just outside the cell is kept up at the full height of the free water and the nitrogen combined immediately upon entering. Even in this case a membrane of 6sq.mm (supposing the cell to be a cube) is scarcely sufficient to allow the absorption in a reasonable time, but the situation is even more unfavourable, because the nitrate will have to come to the cell surface by free diffusion over a mean distance of about 1cm which will take days and keep the nitrate concentration just outside the cell considerably below that of the free water.

Suppose now that we have instead of one cell of $1mm^3$ a thousand cells of $0.001mm^3$ each which we can conceive as cubes of 0.1mm side or still considerably larger than most phytoplankton organisms. These would have an aggregate surface of 10 times the single cell in the first example. Each would require the nitrate from a water volume of $10mm^3$ giving a mean distance for diffusion outside the cell of about 1mm. As the rate of diffusion is inversely proportional to the square of the distance this would mean that the outside conditions would be improved 100 times and with the increase in surface the total improvement of the conditions would be just 1,000 times.

This is, as I said, only an example to illustrate the principle in a general way. The data are still lacking for an exact calculation of the influence of diffusion processes both outside the cells and through their membranes, on the growth rate of phytoplankton organisms, but I believe that an experimental study of this problem on lines related to those so beautifully initiated

by the work of M. H. Jacobs would prove fruitful and help us to understand the conditions determining the utilization of the radiant energy at the disposal of the phytoplankton. As far as I am able to see at present the utilization of light in the sea falls short of that reached on land. In a forest the leaves are arranged to catch the maximum amount of light, and they differ in structure and physiological properties according to their position so that the shaded leaves are able to fully utilize that fraction of light which eventually reaches them. For the phytoplankton an adaptation of this kind has not been demonstrated and is difficult to imagine, because the organisms cannot maintain a definite position with regard to the light. As the intensity of the light falls off rapidly with depth, it is probable that the plankton is adapted generally to a rather low intensity, and it is a fact that where the light is very strong in low latitudes the maximum development of the plankton is reached not in the surface, but at a depth of 25 to 50 meters. This of course means a serious reduction in the total utilization of light.

I have spoken so far mainly of the phytoplankton and must now go on to say a few words about the animal life of the ocean. As on land and everywhere else the animal life depends for its very existence on the assimilation of the plants, but while on land animals of every size up to elephants can partake directly of the food provided by the plants there must be, and is, in the water of the open ocean a special fauna mainly composed of microscopic and just visible animals which are alone able to utilize the small phytoplankton organisms. These in their turn are eaten by somewhat larger animals, and so on right up to the largest fishes. This is of course the only possibility, but it is a wasteful way of doing life's business and means a considerable reduction in the total mass of animals which can be supported on a definite production of phytoplankton food.

The ultimate dependence of the animal life on the invisible phytoplankton is brought out very clearly by a comparison of the blue-water deserts with the greenish areas where water from the deep rises to the surface. In these areas also animal life reaches its maximum development and they become conspicuous especially by the presence of large numbers of whales. The whalebone whales represent the maximum energetic efficiency attained in the ocean. They cannot, it is true, live directly on the phytoplankton, but their main food is small plankton crustaceans and fish which they filter from the water. By instincts which are, as Hjort puts it, "a mystery too deep for mortal man," they are able to find and follow the successive maxima of their food animals and to be "on the spot wherever the harvest is at its height." With what efficiency they work can be seen from their rate of growth which is unparalleled in the animal kingdom. A new-born calf of a blue whale is 7m long and probably weighs about 2,000kg. After 6 to 7 months at the end of the suckling period the length is 16m and when sexually mature at the age of 2 years a whale is 23m long and weighs some 60,000 to 80,000kg.

The whaling industry enables man to obtain his share in the organic productivity of the open ocean, but in the long run only on condition that the limited stock is not unduly depleted as it has been time and again in the history of whaling.

In the introduction to this address I referred to the hosts of animals living in forest soil on the leaves falling from the trees. In the ocean too we have a host of animals living below the zone of assimilation on what sinks down to them from above, but while in the forest the leaves fall only a few meters and become utilized in a layer of a few centimeters, in the ocean the sinking takes places over 4,000 meters on an average and the material has to support life over all this distance as well as in the bottom. To understand how this comes about constitutes one of the most puzzling problems in the energetics of ocean life.

Just below the phytoplankton zone small crustacea abound. They feed on the phytoplankton organisms sinking down to them and in their turn are eaten by somewhat larger animals including fishes, generally of the size of a few centimeters.

So far the situation seems simple enough, but at greater depths where the phytoplankton organisms cannot be of any significance quantitatively, even if a few specimens may come down without being eaten or completely dissolved, there still is a varied fauna including squids and fairly large fishes. Some of these rise towards the surface at night and may feed at higher levels, but many have never been taken at higher levels and certainly spend all their life at depths from 500 to 1,000m downwards. They can be fairly abundant as shown by the fact that the main source of food of the sperm whales seems to be giant squids which live pelagically at depths of 500m. Is it possible that the ultimate food of animals at a certain depth is the small animals and the excreta of animals of the next higher level sinking down to them after death? This would involve a rapid decrease in total organic life with depth, but unfortunately quantitative data which could settle the point are lacking and will be very difficult to obtain.

On and in the muds of the ocean floor there is again a varied fauna with a large number of species comprising representatives of all major groups of marine animals, but as far as present information goes the density of population is very low. It is practically inconceivable that a significant amount of phytoplankton can sink 4km through the masses of water and serve as food for the bottom organisms, the more so as even the shells of small organisms like diatoms become completely dissolved before reaching the greater depths, and the number of microorganisms actually found at great depths dwindle down to almost nothing. But a certain number of large animals must after death become deposited on the bottom as their sinking will be rapid and not require more than a day or two.

It seems possible that the dead bodies of large animals and perhaps their excreta constitute the ultimate food of the abyssal bottom fauna, a conception which would correspond quantitatively to the fauna of the soil living on dead birds, but the possibility first suggested by Alexander Agassiz also seems to be open that a microfauna exists on and in the bottom for which we should have to postulate the ability to absorb dissolved organic substances directly from the water. A serious search for such a fauna has not so far been made, but the organic substances are there, and on these I shall finally have some words to say.

A point of some interest for the economy of life on the earth taken as a whole is the completeness or otherwise of the balance between synthesis and complete breakdown of organic material. By means of the comparatively unlimited supply of energy from the sun organic material is constantly built up out of a small number of inorganic compounds. The supply of certain of these compounds is limited and if there were no breakdown to restore the inorganic compounds the synthesis would soon come to an end for lack of material.

On land, chiefly owing to the concentration of the processes of life mentioned before, the circulation is fairly though not absolutely complete. Living and dead plants and the excreta of animals are vigorously attacked by animals and bacteria, and the organic material which may become permanently deposited in the soil is generally only a small fraction of that which is in active circulation. In fresh waters and in the shallow seas a permanent deposition of organic material takes place in the bottom, but time will not permit me to enter upon a discussion of the mechanism and significance of this. It must suffice to say that lack of oxygen sets a limit to the activity of organisms which would otherwise effect a complete solution and breakdown of the organic material.

In the open ocean the deposition of organic material in the bottom appears to be negligible, but a large quantity is present in solution in the water. The excreta of animals are or become dissolved to a certain extent without being broken down, but what is probably much more important quantitatively is that the dead bodies of microorganisms become to a large extent directly dissolved in the water when sinking down towards the bottom. In the areas especially between 50° and 70° both N and S of the Equator where extremely large phytoplankton maximums occur in the spring and summer the production of organic material is for long periods in excess of consumption and the organisms which cannot be eaten and utilized die off and become dissolved. It has been assumed by Pütter, and observations by Gran and collaborators appear to confirm the assumption, that the plankton algae work in a very wasteful way, losing some 90 per cent of the substances produced by photosynthesis which simply diffuse out into the water. I have tested the point for freshwater algae

where the loss is insignificant (perhaps 5 per cent), but as regards the marine plankton the question is still an open one. The rate at which organic material goes into solution is unknown, but the result: the concentration of organic material in a dissolved state can be ascertained. I have spent a couple of years working out methods for the determination of organic carbon and nitrogen in sea water. These methods have become available quite recently and I have only a single series of determinations representing a column of water of 5,400m length from surface to bottom at a station not very far from Bermuda where the samples have been kindly taken for me by the research vessel "Atlantis" of Woods Hole Oceanographic Institution.

These samples show a uniform content of organic material from the surface down and the concentration of 0.244g nitrogen and 2.36g carbon per cubic meter. If the result is calculated as representing a mixture of "protein" and carbohydrate we find 1.5g protein and 3.9g carbohydrate. This does not sound like a great deal, but it is at least 300 times the total organic dry substance of living organisms found in the sea at any one time.

It follows from this large difference that the quantity of dissolved organic material can only be altered very slowly. The distribution must therefore become almost completely uniform and it is legitimate to take my result as representing not only the column of water from which the samples were drawn, but the ocean as a whole. If we confine ourselves to the Atlantic with an area of 90 million sq. kilometers and a mean depth of 4,000m, we arrive at the total of 5.4×10^{14}kg of protein and 14.4×10^{14}kg of carbohydrate (540 trillion and 1,440 trillion tons respectively), a total which approximates 20,000 times the world's wheat harvest for one year. Are these enormous quantities available as building material and source of energy for the organisms? A German author (Pütter) thought he could show that the dissolved organic material, which he estimated as being even much more abundant than I have found, was indeed the main source of food for aquatic organisms, but his experiments and calculations failed to prove his contention. Very dilute solutions of even the best nutritive material can be utilized only by very small organisms for the reasons stated with regard to the absorption of nitrates by the phytoplankton, and it is to be expected that the dissolved organic material would be available mainly for bacteria and small protozoa.

The recent investigations go to show that the number of bacteria present in ocean water is extremely small and that most of those present are probably associated with larger microorganisms and this fact rather points to the conclusion that the dissolved organic material is not a suitable bacterial food. I referred to the possibility that a microfauna exists in the abysses of the ocean which may be able to utilize the dissolved material, but even if this should on investigation turn out to be more than a possibility the effect upon

the enormous total of this material would be very slight. We have to admit, I believe, that this material has in the main gone out of the organic circulation and represents waste products which cannot be recovered and may be even now slowly accumulating.

I have tried to give you in brief outline the energetics of organic life in the ocean. The picture is very incomplete and probably in some respects faulty, and the reason for this is not only lack of competence on my part, but also lack of data. The ocean problems are many and complicated and a systematic study has been undertaken only for the short span of less than a hundred years. It is a pleasure to record the great part of America in this study from the time of Maury and Agassiz onwards. At the present time both the men and the machinery for an intensive and extensive study of the ocean are available in this great country. I feel confident that their work will solve some of the riddles which now surround us and present us with new and even more interesting problems.

CONDITIONS OF LIFE AT GREAT DEPTHS IN THE OCEAN

By AUGUST KROGH

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When I have accepted the great honour of your invitation and assumed the task of opening a discussion on the conditions of life at great depths in the ocean you have the right to expect that I know something of this subject and have come here to enlighten you about it, but I must confess, and I think it the best plan to do so at the start before you can possibly discover it for yourselves, that I know nothing about it, that I have to offer only more or less vague suggestions. The truth is that the problem has puzzled me for years, that my ideas are still in a rather confused state and that I hope by presenting them to you to obtain facts and clues which may help me to a better understanding. Let me begin by stating some points about the deep sea fauna which I believe to be reliable and relevant facts.

I propose to deal with the open ocean where the conditions can be taken as independent of the land. Here we have in the uppermost strata of the water plankton consisting to a large extent of microscopic plants which are through their assimilation responsible for the whole of the organic material produced in the sea. Along with these producers are many animals feeding directly, or indirectly by taking smaller animals as their food, on the phytoplankton and breaking down through their metabolic processes the surplus of nutritive substances produced by the plants. Down to a variable depth which very rarely exceeds 200m assimilation is on the whole in excess of dissimilation and the surplus is produced which has to serve the needs of all organisms at greater depths. Below 400m there is never sufficient light to permit any assimilation and at greater depths absolute darkness prevails except for the faint light emitted from fishes and a few other organisms.

The number and total mass of organisms decreases very rapidly with the depth. This has been established again and again both for netplankton and for nannoplankton organisms and is well illustrated by figures given by Hentschel for the number of nannoplankton organisms present in 1 liter of ocean water in the area 0-10°S and 10-20°W in the Atlantic.

Surface	10100	1000m	90
50m	9400	2000	50
100	2700	3000	18
400	260	5000	15

At 2000m the number is reduced to 0.5 per cent and a further reduction takes place with increasing depth. No figures exist for the large organisms like cephalopods, fishes and cetaceans, but it is well known that cephalopods and

cetaceans have not been found at great depths and there is no doubt that the number and total mass of fishes is greatly reduced.

On and in the bottom muds a highly varied fauna is present. This comprises representatives of all major groups of marine animals. Let us consider for a moment the conditions under which these animals live. The mean depth of the Atlantic is 3900m and over a fourth of the area of 90 million sq. kilometers the depth exceeds 5000m. Complete darkness obtains. The pressure increases about one atmosphere for every 10m and is at the mean depth about 400kg. per sq. cm. The temperature is constant at the bottom the whole year round and varies over the vast Atlantic only from 0-3°C. Although the water is probably never absolutely quiescent the currents are extremely slow, being estimated by Helland-Hansen to be of the order of one to a few centimeters per second, say 25 to 100m per hour. Oxygen is available everywhere, except in a few excessively deep holes, in quantities of 5-6cc per liter. This shows that the water is renewed at a rate well in excess of the oxidative breakdown of oxidizable substances.

How do these conditions affect the bottom organisms? The species and genera are on the whole nearly related to the corresponding forms of intermediate and shallow depths. There is, as far as I have been able to find out, especially from the narrative and summaries in the Challenger reports, no general feature characteristic of the fauna of the greatest depth.

It is stated that the tissues of many deep sea fishes are of a very loose texture when examined at the surface and it was assumed that the enormous pressure at their habitat would render them more firm. Later investigations have failed to confirm the statements and I can find no reason for the assumption. The pressure will act on the fish tissue in almost exactly the same way as on the water itself, reducing the volume by a little less than 2 per cent at 400 atmospheres. One might suppose that such a compression would considerably increase the internal friction or viscosity of the water, but according to the measurements of physicists this is not the case. The viscosity of pure water is even somewhat reduced by high pressure at temperatures below 32°C The pressure is probably a factor of slight if any significance except for fishes possessing a swimming bladder.

The absence of light also appears to affect animals very slightly—if at all. The low and uniform temperature is a factor of considerable importance from my point of view. The metabolism of invertebrates, and of coldblooded animals generally, is closely correlated to temperature. The resting metabolism of any given animal is a simple function of temperature increasing with temperature according to a definite curve. At 0°C the metabolism of coldblooded animals is generally only about a fifth to a sixth of the metabolism at 10°C. The quantity of food necessary to maintain life is therefore considerably lower at great depths although not necessarily quite so low as indicated by the figures for the resting metabolism.

The density of population on the bottom is practically unknown and I would strongly urge the adoption of quantitative methods to investigate this very important problem. The *Petersen* apparatus for taking bottom samples of 0.2 or 0.1 sq. m. has been successfully used by Spärck in depths of 1100m and I can find no reason why it should not be able to work at any depth.

From the dredging and trawlings of the Challenger and other expeditions it can be concluded that the number of individual animals living at great depths is small only. When a trawl going over 10.000 sq. m. of bottom catches 200 specimens the haul is considered exceptionally successful and in such a haul 50 or more species of Spongia, Actinia, Echinodermata, Annelida, Crustacea, Lamellibranchia, Gasteropoda, Polyzoa, Brachiopoda and fishes may be represented.

The working of trawls and dredges at great depths is uncertain and fitful, and it must not be assumed that even the best will take from the area covered all the animals which are large enough to be held by the meshes of the trawl. On the other hand, when on similar bottom certain large areas give on an average much fewer specimens per haul than others it must be legitimate to conclude that the average density of population is actually lower in the first. It is therefore almost certainly significant that the average trawling on the Globigerina ooze gave in the Atlantic 21 specimens, in the Pacific 56 and in the Southern Ocean 97. This points to a correlation with the density of surface life and a corresponding correlation has been definitely demonstrated for the bathypelagic fauna. Hensen first established the surprising fact that the plankton of the upper strata of the Ocean is much more abundant at high latitudes where cold water comes to the surface than in the tropics, and Hentschel showed conclusively that the density of nannoplankton organisms at 2000m depends upon the density at the surface. In tropical areas with less than 5000 organisms per liter at the surface the number at 2000m is almost always below 10 per liter, whereas in areas with over 200,000 per liter at the surface the figure for 2000m exceeds 100 and may reach a maximum of 200.

In regard to the ultimate food supply of the abyssal fauna there are two main possibilities to consider.

1. Surface organisms, their excreta and remains sink down through the water and are eaten as such by the bathypelagic and bottom animals.

2. The nutritional substances of surface organisms become dissolved in the water and as the waters are gradually, but very effectively, mixed—as shown by the oxygen content of the water at great depths—the solution can serve as a source of nutrition for the abyssal fauna.

The first possibility receives strong support from the fact just cited of the dependence of the abyssal fauna upon the flora and fauna immediately above it, but it cannot be denied that in spite of that the conception presents great difficulties.

As shown by the investigations of Hensen, Lohmann, and Hentschel only

a very insignificant fraction of the phytoplankton organisms can ever reach great depths. Some are intercepted on the way down by the organisms of intermediate depths, especially by the comparatively rich fauna of crustaceans, cephalopods and fishes living between 500 and 1000m, and those escaping this fate must become to a very large extent dissolved in the water. In 500m already the diatom shells are usually empty, but even below 3000m a few are found containing remains of the protoplasmic content. Almost the whole of the calcareous or siliceous shells of foraminifera and diatoms even disappear by going into solution before they reach the bottom at depths beyond 4500m.

The nannoplankton found below 2000m represents less and in most cases much less than 2mg of organic substance per m^3 of the water and even assuming a fairly rapid reproduction the value of such organisms as food for the bottom fauna is negligible, the more so as the rate at which they can reach the bottom must be very slow. At the same time there can be no doubt that phytoplankton organisms do serve as food for the bathypelagic fauna. Chun has found the large radiolarians living below 3000m often filled up with diatom shells, and the species of Copepoda and Ostracoda leading a pelagic life in these depths can exist only by feeding on small organisms.

The excreta and dead bodies of larger animals do not appear to have been seriously considered as food of the bottom fauna. Of course their concentration and total mass in the upper strata of the ocean is small compared with that of the phytoplankton on which their existence depends, but this is set off by their velocity in sinking through the water. There is no question of a whale or even a fairly large fish becoming dissolved by the water on its way down and even the chance of its being eaten before reaching the bottom is slight once the uppermost strata are passed. A sinking velocity of 100m per hour will bring a body to the bottom in most places in less than 2 days. At one station in the southern Pacific the Challenger got up in the trawl from the red clay bottom in 4300m several thousand sharks teeth and not less than 50 earbones of whales, but of course it is not known how many thousands of years this accumulation required. In this case, as in the whole problem, the data on which to base a quantitative consideration are sadly lacking. Quite recent calculations by Hjort and collaborators which are admittedly very rough approximations put the number of whales present in the Antarctic Ocean in an area of 8 million sq. km. at approximately 300,000 of which in a state of equilibrium the birth and death rate should approximate 50,000 pro year. If all these reached the bottom within the area considered it would mean 1 whale yearly on 160 sq. km. (= 50 sq. miles). It does not sound like much, but still it corresponds to half a gram of animal food per sq. m., and it seems doubtful whether the total of the animals living on the bottom at great depths can amount to much more. This calculation should not of course be taken too seriously, but it does, I think, make it practically certain that the bottom fauna must obtain a more than negligible amount of food from fairly large

animals sinking down from the surface. Whether or not this can be sufficient to maintain the fauna or can provide perhaps only a fraction of their food requirements we do not know. If insufficient it must be supplemented from some other source and the only one available is the dissolved organic material present in the ocean water. In a certain sense this source is enormously rich, but in spite of that it is doubtful whether it can be utilized to any but a very slight extent.

I had hoped to be able on this point at least to give definite information as a basis for discussion, but all I can do is to give some preliminary figures for the amount of dissolved organic material, which may or may not be quite accurate. The determination of organic material dissolved in sea water is a very difficult proposition technically owing chiefly to the relatively enormous quantities of salts present along with it. Assuming for instance that we have 3.5mg of organic material per liter, this is found mixed after evaporation to dryness with 10,000 times its weight of salts. For freshwaters I have worked out a dry combustion method capable of dealing with one liter of water which is evaporated down by stages, finally in a combustion tube. This yields by combustion organic carbon as CO_2, nitrogen as gaseous nitrogen, and in addition allows the determination of the volume of oxygen necessary to complete combustion, so that the caloric value and, under certain assumptions, the composition of the material can be calculated. By means of this method I found the organic material present in true solution in the water of a Danish lake to be about 9mg per liter with a combustion value of 42 gram-calories and consisting of 3.3mg of "protein" and 5.5mg of carbohydrate.

Applied to sea water this method fails completely, and I have found it necessary to work out methods of wet combustion. After two years of experimentation I believe that I have in the main succeeded, although the controls have not yet been completed to my satisfaction. I shall give a brief outline of the methods as now employed. Organic carbon and nitrogen only are determined on separate small samples of water not exceeding 20cc.

For the nitrogen determinations I of course tried first to utilize the Kjeldahl method, but after a very large number of trials the attempts had to be given up. The large amount of salts present necessitates the use of a volume of sulphuric acid very large in proportion to the organic material, and the acid could not be purified sufficiently. It contains, even after repeated distillations and heating of the vapour with oxygen to 900°C an incontrollable amount of an unknown substance, and yields variable quantities of ammonia by the Kjeldahl method. I now utilize a modified Will-Varrentrap method by which the water is evaporated down with a surplus of alkali in a silver combustion tube and the residue heated in the same tube to a dull red heat. This converts the organic nitrogen into ammonia, but in order to drive off all the ammonia, a large fraction of which becomes occluded in the salt, water must be added and the solution once more evaporated. The ammonia is taken

up in a weak acid and determined by means of a special titration which is extremely sensitive and fairly accurate. I shall give the results obtained on a number of samples from the Atlantic at 30°N and 69°W where the depth is about 5400m, kindly taken for me on board the MS. "Atlantis" of the Oceanographic Institution, Woods Hole.

Surface	1000m	2000m	3250m	4250m	4750m
0.378	0.275	0.265	0.249	0.273	0.261mg/1

With the exception of the value for the surface these figures are identical within the limits of error of the method. The results include the preformed ammonia which can be determined separately by distilling off a 20cc sample of water made just alkaline (pH 9.0).

Surface	25m	1000m	2000m	3250m	3750m	4250m	4750m
0.120	0.036	0.027	0.025	0.021	0.024		0.023mg/1

These determinations have given the following results:
The values for the samples from 1000m downwards are again identical and when these are subtracted from the total N values the following figures result for the nitrogen in organic combination:

Surface	1000m	2000m	3250m	4250m	4750m
0.258	0.248	0.240	0.229	0.250	0.238mg/1

These figures show that all the water from the surface down to the bottom contains the same amount of organically combined nitrogen. The average is 0.244 ± 0.010.

Carbon determinations have been made by means of wet combustion with sulphuric acid and chromate. In this case also the organic material present in all samples of sulphuric acid has given much trouble, but owing to the much larger amount of carbon present in the water the errors are less disastrous when a specially prepared acid is used. It is necessary for this determination to get rid of most of the chlorine present in the water and this can be done by precipitation with thallium sulphate. The filtrate from 20 cc is evaporated down to dryness in a basin at a fairly low temperature, transferred to a special distillation flask and heated to 120°C with the chromate mixture under a slow current of CO_2-free air. Some carbon monoxide may be formed in the reaction and a little chlorine is always liberated. The air must therefore be taken through a combustion tube at 400° with "molecular silver," platinum and copper oxide. The CO_2 is absorbed in about 0.5 cc. of baryta solution which is micro-titrated afterward with n/3 HCl. On the water-samples mentioned above I have obtained the following results:

25m	2000m	3250m	3750m	4250m	4750m
2.40	2.35	2.32	2.36	2.17	2.48

= Average 2.35 ± 0.09mg/1

Here again the values are identical within the limits of error of the method.

If the figures of 0.244mg organic nitrogen and 2.35mg organic carbon per liter are accepted for the 5.4km vertical column of water represented in

the samples they show the presence below 1sq.m. at this particular spot of 1.3kg of organic nitrogen and 12.7kg of organic carbon and there is every reason to believe that the same figures are valid for the whole mass of Atlantic water. The quantity is namely at least three hundred and probably more than a thousand times larger than that which is present in all marine organisms at any one time. I arrive at this estimate in the following way.

In Hensen's chart showing the track of the Plankton Expedition he gives the number of cubic centimeters of plankton taken by the vertical net of 1/10sq.m. from 2-400m depth to the surface. Putting the net factor as 2 (1.8 according to Hensen) and the mean depth as 300m each haul represents 15m³ of water. The maximum catch is 140-200cc of moist plankton and the mean about 12cc—say 1cc per m³. The dry organic substance in the wet plankton is certainly below 5 per cent of which at most 1/2 is carbon; say 25mg C per m³.

Figures for the nannoplankton are given by Lohmann, who finds in the upper 25m in the warm water of the tropics 2500 cells and in the cool water 21,000 cells per liter. Taking the dimensions of the cells represented in the largest numbers I arrive at a mean volume per cell of 6×10^{-5} mm³ or for 1m³ in the tropics 150 mm³ and in the cool water 1300 mm³. I put the mean as 500 and assume the same content down to 300m which is to overestimate it greatly. Assuming for these organisms 10 per cent organic dry substance they also give 25mg of carbon per m³. Adding the two figures together in spite of their undoubted overlap and allowing 20 per cent more for large animals I arrive at the figure 60mg carbon for the organisms of 1m³ from the surface to 300m. The maximum observed in the waters south of Greenland should correspond to about 600mg of carbon per m³. At 300m the plankton quantity is about 10 per cent of the value for the upper strata, while at the bottom (4000m) it sinks practically to zero, and this means for the whole mass of water from surface to bottom a concentration about 7.3mg of carbon per m³ in organisms of all kinds. This is 1/300 of the organic carbon in solution.

It follows therefore that changes in the quantity of dissolved material brought about by organisms must be extremely slow and gradual and that local differences, if any, must fall within the limits of error of the rather crude analytical methods.

It must be admitted that my figures in spite of their agreement may have some systematic error which is not, however, likely to be large. Accepting them as they stand and assuming that they represent a mixture of amino acids, which may be designated as "protein," and carbohydrate they indicate a content per liter of 1.5mg "protein" (=0.8mg C) and 3.9mg carbohydrate (with 40 per cent carbon). This is the most favourable assumption from the point of view that the dissolved substances are to be utilized as nutrition. It is more probable really that a certain portion of the nitrogen is combined in waste

products which cannot be utilized by animals and that another fraction of the organic material consists of "humus" which seems to be very resistant to the attack of organisms, including bacteria.

Even so the quantity of nutritive material *present* in solution in the water should be many times larger than that available in organisms and their excreta, but the problem is: To what extent, if any, are these substances available as animal food. Pütter's well known view, which he sought to establish by a large number of experiments and ingenious calculations, was that the dissolved organic substances were freely available to all aquatic organisms, including crustaceans and fishes, and constituted their main source of nutrition. In this form the hypothesis is not only unproven, but definitely has been shown to be erroneous. Animals like crustaceans and fishes are unable to take up significant amounts of organic material from a very dilute solution. The chitinous integuments of crustaceans and the gills of fishes are practically impermeable to the substances in question. If they were freely permeable the animals would not gain but lose protein and carbohydrate from the much higher concentrations present in their blood. If a unidirectional permeability is postulated the concentration in the water is too low to be of any avail for animals above a certain small size. This last argument holds also for a very large number of invertebrates generally.

There is little doubt according to experiments and observations by Gilbert Ranson that lamellibranchs for instance can take up substances through their gills even from rather dilute solutions, but the rate will be too slow to cover more than a fraction of their metabolism, and experiments made in my laboratory on freshwater forms seem to show that the gain from this source is more than counterbalanced by a loss of organic material going into solution.

The utilization of organic material in dilute solution depends largely upon surface in relation to volume. Disregarding specially developed surfaces like gills or tentacles this relation is a question of size, the smallest organisms having the largest relative surface. Nobody doubts that bacteria can and do take up their nutrition directly even from very dilute solutions like ordinary distilled water containing only about 1mg of organic material per liter. I have not been able to find reliable information in literature as to the quantitative significance of bacteria in the bottom deposits of the ocean. In the ocean water the number of bacteria appears to be small only, and according to the recent very interesting studies by Waksman and his collaborators from the Gulf of Maine the bacteria seem to be closely associated with the phytoplankton organisms. To my mind this furnishes rather a strong argument against the nutritive value of the organic material present in solution.

Beyond the bacteria the protozoa and especially the naked forms should be able to utilize dilute solutions of organic material, but if they really do so is an open question. Many at least do not thrive in cultures without solid food in the shape of bacteria and other microörganisms.

A. Agassiz said in 1888, "There must be all over the bottom on which reticularian rhizopods have been found, thousands of undiscovered minute protozoans which have no solid tests." As far as I am aware such forms still remain undiscovered, although it should not now present unsurmountable difficulties to take up the study of the micro-fauna of the bottom at all depths both from a morphological and a quantitative point of view.

Finally there are the sponges which are known to occur all over the ocean bottom and in certain localities may be present in considerable quantities. From their enormous surface development the sponges would be considered well adapted to utilize dissolved food. Pütter thought he had shown that dissolved substances were their chief source of nourishment, but his experiments are certainly inconclusive. On the other hand if sponges cannot utilize the dissolved material, how do they obtain sufficient food? They are fixed on the bottom. They can only retain the smallest organisms and particles floating in the water. Can the "rain" of microörganisms and detritus hitting them from above be sufficient for their requirements? I find in the Challenger narrative the statement that deep sea sponges are often filled with diatoms and radiolarians "although the bottom at these stations was not a diatom or radiolarian ooze," but even in the face of this statement I find it very hard to believe that sufficient food in the shape of microorganisms can arrive directly from above. Is there on the bottom itself a production of microorganisms and particles and can the slow currents lift them and carry them along for the benefit of the larger sponges and polyps of which some rise to considerable height above the bottom (the hydroid Monocaulus to 2m)?

Are we to assume the existence of a benthopelagic fauna of organisms possessing active locomotion and inhabiting the water just above the bottom? Sexual products and larvae of many of the bottom organisms must in all probability go to make up such a fauna, which would, I think, be well worth looking for.

From the feeding habits of a considerable number of the abyssal animal forms it is, I think, necessary to conclude that food must be available as minute particles or organisms, or both, in the ooze as well as in the water just above it. The deep water Elasipodae among the Holothurians crawl about slowly on the bottom and are mentioned in the Challenger narrative as having their alimentary canals always highly distended by bottom material, which must therefore contain nutritive substances at least in the superficial layer. Hertwig in commenting upon the conversion in deep water Actinia of the tentacles into suctorial tubes supposes that these are more useful for absorbing matters "far advanced in decomposition and suspended in water or embedded in mud."

There are quite a number of animals belonging to several groups (Bryozoa, Annelida, Actinia) which have their tubes or colonies fixed to manganese nodules on the surface of the "red clay" at the greatest depths. These must

live on minute organisms or particles. It seems therefore probable that such organisms must be present, although the methods so far employed have failed to detect them, and the possibility can not be excluded that they in their turn obtain their nutriment directly from the water.

This is, perhaps in too many words, my conception of where we stand at present. The problem resolves itself into a number of queries. If my words mean anything at all, they mean a plea for answers to some of these queries. Answers which can be obtained by studies in nature and in the laboratory.

PARTICULATE AND DISSOLVED ORGANIC MATTER IN INLAND LAKES*

By E. A. BIRGE and C. JUDAY

Introduction

The Wisconsin Geological and Natural History Survey has given much time to the investigation of ecological conditions in inland lakes, with especial reference to the amount and production of actual and potential food materials. Since 1924 its main activities have been concentrated in the Highland Lake District, lying in the northeastern part of the State; this work furnishes the basis for the present paper.

A sketch map of the District appears in Figure 1; a more detailed map is given in the report on The Hydrography and Morphometry of the Lakes (Juday 1914) and in The Highland Lake District of Northeastern Wisconsin and the Trout Lake Limnological Laboratory (Juday and Birge 1930).

The District is shield-shaped or triangular in area with its base along the north boundary of the State, where it extends into Michigan for a distance of six to ten miles (10-16 km.). The apex is at Tomahawk; the general east-west breadth near the north margin is about 60 miles (96 km.) and its height is about the same, measured from Tomahawk at right angles to the first line. The area is about 3,000 square miles (7,800 sq. km.).

The District is essentially an elevated overwash plain of glacial drift, with low ridges of recessional moraines rising above it. The underlying rock is deeply buried with drift (40-70 m.); exposures of rock are rare and the lakes are in basins left by melting ice-blocks. The drift is mostly sand or gravel and much of the drainage is underground, a fact of great importance in the economy of the lakes; it contains varying amounts of calcareous material.

The map shows that the lakes are numerous, but only a small part of them appear on it. This paper reports the general results from an examination of 529 lakes, all lying within a radius of 25-30 miles (40-50 km.) from the Laboratory. About a dozen of these are pools or lakelets situated in the middle of bogs, but no serious attempt has been made to examine the almost innumerable waters of this type.

The lakes of the District differ greatly in area, depth and character. The largest is Lac Vieux Desert, the source of the Wisconsin River. It has an area of 4,800 acres (1930 ha.). Trout Lake has the greatest depth, namely 117 feet (35 m.). In general the water of these lakes is soft; the bound carbon dioxide ranges from 0.2 to 35 mg/1. Lakes in the southern part of the State, like Lake Mendota, have an average amount of bound carbon

* This paper was presented to the meeting of the Ecological Society of America in two parts, as indicated below. Since both parts had the same data in view, they are here combined for publication.

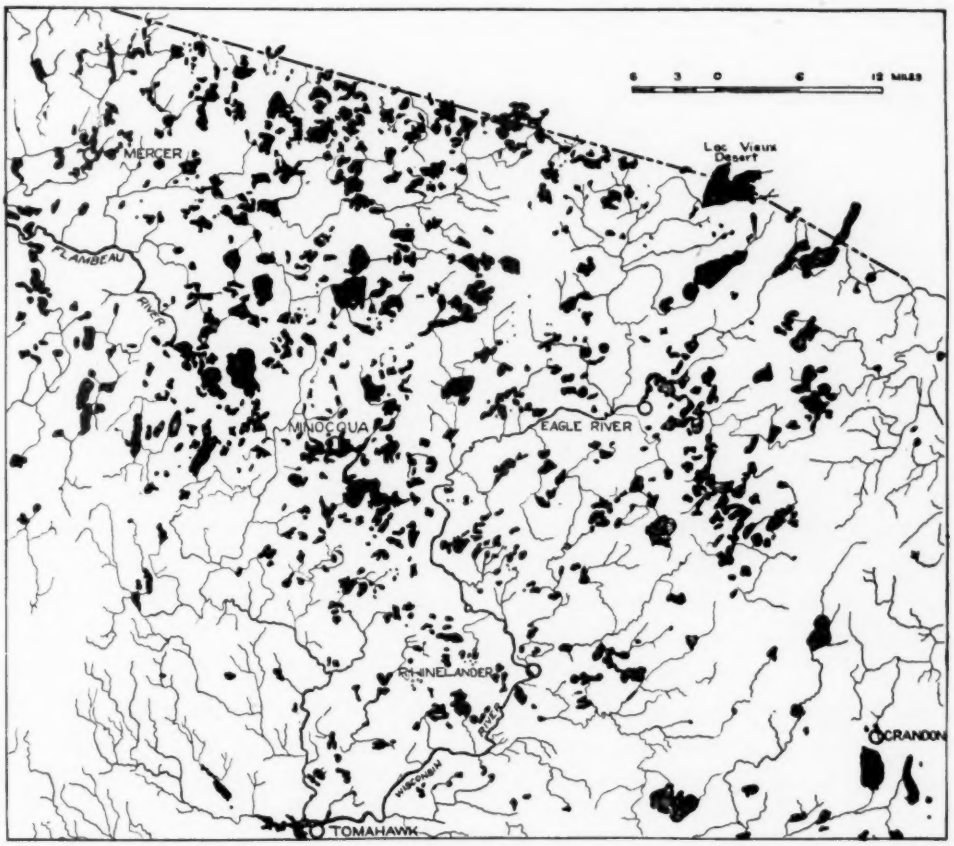

FIG. 1. Sketch map of the Highland Lake District of northeastern Wisconsin. Many lakes are too small to be represented on a map of this scale. Vieux Desert Lake is the large lake which is crossed by the northern boundary of the state. Trout Lake is the large lake in two parts, lying about one-third of the distance from the northern and the western boundary of the map. The Laboratory is on the east side, on the point which nearly divides the lake.

dioxide that is about twice as large as the maximum in the District. The specific conductance of the water, which is proportional to the total electrolytes present in it, ranges from a minimum of 6 to a maximum of about 150 reciprocal megohms. Ordinary distilled water has a conductance of about 4 reciprocal megohms, so that few small natural bodies of water are poorer in electrolytes than are some of these. The specific conductance of the waters of southern Wisconsin lakes ranges from about 230 up to 350 reciprocal megohms.

The hydrogen ion concentration also covers a wide range in these lakes; it varies from pH 4.4 to pH 9.4. The calcium content of the water differs greatly in the different lakes; it varies from a minimum of 0.2 mg/1 to a maximum of 20 mg/1, which represents a difference of a hundredfold.

These lakes may be classified into two types; those with outlets and those without them. Lakes of the first type are connected with the surface drain-

age of the District and are called *drainage lakes;* the movement of water through lakes of the second type is entirely under ground and they are named *seepage lakes.* In the list of 529 lakes, there are 291 drainage and 238 seepage lakes; but this division is not wholly exact, since lakes occur that might be classed as drainage because of temporary outlets or as seepage because the outlet only rarely carries water.

In general the two types of lakes are sharply distinguished. Seepage lakes have little dissolved inorganic matter; their organic matter, including plankton, is less than that of the drainage lakes. Their water is usually, but not always, more transparent than that of drainage lakes and it is ordinarily less stained by extractives from bog material. Thus the two types offer habitats that differ widely in important characters.

There can be few regions in the world that offer ecological habitats so numerous, so accessible, so separate from each other, and with such a range of characters. The District provides an enormous number of what may be called natural experimental basins. These are now in their natural conditions and are likely to remain so. The original forest has been cut and the land is now covered with thick-set second growth trees. The soil is poor; little of it is cultivated now, and the cultivated area is not likely to increase. Manufactures are practically absent, so that there is no pollution of lakes and streams from this source. Thus the present situation will probably continue for a long time and the lakes will furnish an unaltered environment for life.

In view of such conditions in the District, the Survey undertook, as its first task, to make a sort of general inventory of the lakes, recording the most important facts of their chemistry, physics, and biology. Those data were determined which were most readily available for such an inventory and which would serve as a basis for other and more detailed studies.

The present paper offers a summary view of part of these data, as a contribution to the subject under discussion at this meeting. It is not a full summary of the ascertained facts regarding the District, nor is it an introduction to a full report. Data from lakes situated in other parts of Wisconsin are presented for comparison or interpretation. It should also be added that some few chemical analyses still remain to be done. It is therefore quite possible that the full report, when completed, may show small changes in the mean results here given; but we do not anticipate changes which will seriously affect any general conclusions that may be drawn from data herewith presented.

PART I

THE CENTRIFUGE PLANKTON CONTENT OF THE WATER

By C. JUDAY

From a food standpoint, one of the very important elements in the environment of many of the larger aquatic animals inhabiting the waters of the Highland Lake District is the particulate material which can be separated from the water by means of a centrifuge. This material consists of microscopic plants and animals, both living and dead, known as the plankton, and of centrifugible organic particles derived from these organisms and from other sources. As originally used, the term plankton referred chiefly to the larger microscopic forms which can be obtained by means of nets with silk gauze straining surfaces; subsequent studies carried on by means of centrifuges and filters have shown that many of the plankton forms are so small that they readily escape through the meshes of such nets. The quantity of material lost by nets, in fact, may be several times as large as that which is retained. The most recent investigations have demonstrated that there is not only a wide range in the size of the living plankton organisms, but that there is also a continuous series of changes ranging from the complete lifeless bodies of these microscopic forms down through various stages of disintegration into smaller and smaller particles which finally terminate in substances that pass into true solution. Thus through its decomposition, the plankton makes a direct contribution to the dissolved organic content of the water and it also affects the dissolved oxygen and carbon dioxide content of the water through the processes of photosynthesis and decomposition.

The importance of plankton as a phenomenon of aquatic life itself and as a source of food for other aquatic forms has led to extended qualitative, quantitative, and chemical studies of it and of the various products which it yields. Various types of nets, centrifuges and filters have been used for the quantitative studies, but each of these instruments has its limitations as well as its advantages. Nets lose the smaller organisms, while centrifuges and filters remove some of the larger particles of disintegrating individuals as well as the whole organisms. The shortcomings of the latter instruments, however, are not serious, since the extra organic material obtained by them has its origin chiefly in the plankton in many cases.

The quantitative study of plankton is a very complex problem. This is due to the great variety of the organisms involved and to differences in their size and in their rates of reproduction; also growth and reproduction as well as losses by death and consumption for food go on continuously throughout the year. There is no definite time when one crop of plankton ceases and another begins. Thus the planktologist must be content with what has been called the "standing crop." This can be obtained by making regular quanti-

tative observations over a considerable period of time; the rapid multiplication and the equally rapid decline of some of the plankton constituents at times produce wide fluctuations in the crop, so that observations must be continued long enough to obtain a fair average of the standing crop.

APPARATUS AND METHODS

The Foerst electric centrifuge was used for securing plankton material from the waters of the 529 lakes of the Highland Lake District that have been studied. Experiments have shown that this instrument removes 95 per cent or more of the particulate material that is larger than bacteria, as well as 25 to 50 per cent of the latter. Two catches were made from each sample of water; one consisted of the centrifuge material from a liter of water which was used for a gravimetric determination and the other that from either a liter or a half liter of water which was used for a numerical study. The former catch was transferred to a dish, evaporated to dryness, weighed and then ignited in order to ascertain the amount of dry organic matter in the centrifuge plankton, as represented by the loss on ignition; blanks of the centrifuged water were run and corrections were made for the loss of carbon dioxide from the carbonates and also for the organic matter dissolved in the water. The second catch was preserved in formaldehyde and used for a numerical study of the various forms that were present. The larger constituents, such as the crustacea and the rotifers, were not abundant enough for numerical determination in the liter or half-liter samples, so that it was necessary to use a 10 liter plankton trap for a study of the abundance and vertical distribution of these forms.

The work has been carried on chiefly during the summer months and the results give a general idea of the centrifuge and trap plankton during this season of the year. A few of the lakes have been visited regularly for eight summers, but the great majority of the 529 lakes have received only one to five visits in this interval of time.

CENTRIFUGE PLANKTON OF SURFACE WATER

In the course of these investigations, centrifuge catches have been obtained from 1,051 surface samples. Of this number 332 were single observations on each lake, while the others represented from 2 to 48 catches on each of the remaining lakes. The largest number (48) was obtained from the surface of Trout Lake. The dry organic content of these surface centrifuge catches varied from a minimum of 0.23 mg/l in Long Lake by Mc Naughton to a maximum of 12.0 mg/l in Brazell or Allen Lake. Long Lake belongs to the seepage type and has very soft water; the specific conductance was only 11 reciprocal megohms and the total residue 15 mg/l. Brazell Lake belongs to the drainage type; the conductance of the water was 62 reciprocal megohms

and the residue 107 mg/1. This catch from Brazell Lake was obtained with a Sharples supercentrifuge and a sample of 100 liters.

Approximately half of the 1,051 surface samples yielded less than 1.0 mg/1 of dry organic matter and 75 per cent of them were less than 1.5 mg/1. Only 11 of them contained as much as 5.0 mg/1 or more. The mean quantity of dry organic material found in all of the surface samples was 1.29 mg/1.

When the surface catches are grouped by lakes, the centrifuge plankton ranges from a minimum of 0.23 mg/1 in Long Lake at Mc Naughton to a maximum of 9.18 mg/1 in Brazell Lake. Two samples were obtained from the latter; one of them yielded 6.36 and the other 12.0 mg/1. The mean quantity of dry organic material in the surface centrifuge catches was less than 1.0 mg/1 in 40 per cent of the lakes and less than 2.0 mg/1 in 85 per cent of them. The mean quantity for the 529 lakes is 1.36 mg/1.

From a theoretical standpoint, there should be a correlation between the yield of centrifuge plankton and the chemical characteristics of the various lake waters. That is, the hard water lakes, in general, should be more productive than the soft water ones. Direct correlations of this character have not been established in many cases, however. Waters with minimum amounts of dissolved substances are even more productive in many instances than those with much larger amounts. In fact, the lakes which do not show a direct correlation between the plankton yield and the quantity of dissolved material in the water are substantially as numerous as those that do show it.

Crystal Lake, for instance, with an average specific conductance of 9 reciprocal megohms, yields a small plankton crop; the average organic content of 11 surface samples was 0.55 mg/1. In Sterrett Lake, with a mean conductance of 14 reciprocal megohms, the mean quantity of organic matter in 6 centrifuge catches, taken in different summers, was 2.1 mg/1, or substantially four times as much as was found in the surface water of Crystal Lake. In Wild Cat Lake, with a conductance of 100, the mean amount of dry organic matter in 8 surface samples was 1.57 mg/1; Arbor Vitae Lake, with a specific conductance of 94, yielded an average of 1.61 mg/1. Crystal Lake is deep enough to be thermally stratified in summer, so that the dissolved substances of the hypolimnion are not in general circulation at this time. Sterrett Lake is shallow and the water is kept in circulation at all depths during the summer, so that the dissolved substances may be used repeatedly by the phytoplankton as the season progresses; some of these solutes are the decomposition products of plants and animals found in the lake, some are extracted from the bottom deposits and others are derived from rain and ground water. Arbor Vitae Lake, likewise, is so shallow that the wind keeps its water in complete circulation during the summer, but its crop of phytoplankton falls below that of Sterrett Lake in spite of the fact that its water

contains a much larger quantity of dissolved material than that of the latter. Only a very small area of Wild Cat Lake is deep enough to become stratified in summer, so that it presents essentially the same conditions as Arbor Vitae Lake. Mann Lake is similar in depth and hardness to Wild Cat and Arbor Vitae lakes, but it produces a much larger average crop of plankton. Mann Lake is only 1-2 m. deep and it is fed by rather large springs, so that the renewal of its water is somewhat greater than that of the other two lakes; this may have a more or less marked effect upon its productivity. Some of the shallow soft water lakes produce small crops of plankton like Crystal Lake and others produce more abundant crops like Sterrett Lake; thus the results show clearly that other factors besides the dissolved substances are involved in the problem of plankton production.

SEASONAL AND ANNUAL VARIATIONS

The observations on the centrifuge plankton have been confined principally to the summer months; that is, from late June to early September. In addition also, samples were obtained from 3 of these lakes in the month of February, from 32 in April-May, from 4 in October and from 3 in November, so that December, January and March are the only months not represented in the data.

With respect to the seasonal variations in the amount of centrifuge plankton, the minimum for 48 surface samples of Trout Lake was 0.40 mg/1 on April 12, 1931. A summer minimum of 0.55 mg/1 was observed on July 17, 1925. The maximum quantity was obtained on June 25, 1926, namely 1.33 mg/1, while the next largest amount (1.23 mg/1) was noted on October 9, 1932. The mean of the 48 surface samples was 0.90 mg/1. Thus there was somewhat more than a threefold range in the quantity of dry organic matter in the centrifuge plankton of Trout Lake.

The February catches yielded a smaller amount of organic matter than the means of the three lakes from which they were obtained, but they were not the smallest amounts obtained from these lakes. In 14 of the 32 lakes on which surface samples were obtained in April-May, the spring catches yielded the maximum amounts of centrifuge plankton for the respective lakes, but in the other 18 lakes the spring samples yielded less than the summer samples of the same lakes. In most cases, the spring visits to these lakes were made soon after the ice had disappeared from them, so that the vernal growths of plankton were in progress at the time of the visits.

During the progress of these studies, 35 sets of observations were made in late June and early July, and again in August of the same summer on 12 different lakes. In these early and late summer catches, the largest percentile difference in yield of centrifuge plankton was noted in Crystal Lake where there was substantially a threefold difference, the amount ranging from 0.27 mg/1 on June 26, 1926 to 0.80 mg/1 on August 17, 1926. In the

other 11 lakes on which such observations were made, the differences were greater than twofold but less than threefold in three of them, while all of the others were less than twofold. In 17 of the 35 sets of observations, the quantity of plankton was larger in late June or early July than in August, but in the other 18 sets the reverse was true.

Regarding annual variations in the quantity of plankton, catches were taken from the surface water of 205 different lakes in two or more summers. The differences in the yield of plankton from year to year ranged from none to a maximum of eightfold. Only 39 lakes showed differences amounting to threefold or more and only 15 reached fourfold or more. In the great majority of them, therefore, the annual variations in the quantity of plankton found in the surface water were within the range of the seasonal variations. The maximum difference was found in Jag Lake, where the minimum quantity of dry organic matter in the centrifuge plankton was 0.30 mg/1 and the maximum amount 2.61 mg/1, slightly more than an eightfold difference. Little or no difference in annual yield was noted in a considerable number of lakes.

DRAINAGE AND SEEPAGE LAKES

The plankton yield of the drainage lakes was considerably larger than that of the seepage group. The mean quantity of dry organic matter in the surface catches of the former group was 1.58 mg/1 and in the latter 1.09 mg/1. Thus the average plankton content of the drainage lakes was about 45 per cent larger than that of the seepage lakes. These results were obtained from 291 drainage and 238 seepage lakes. This difference is large enough to be of considerable significance. Only half as many drainage as seepage lakes yielded less than 1.0 mg/1 of centrifuge plankton and similar differences were noted in the larger yields of plankton. From these results, it appears that the more active exchange of the water content of the lakes having outlets has a very important effect upon their plankton production. The seepage lakes, being without inlets or outlets, are strictly dependent upon their own resources for the dissolved mineral and other constituents which are used as the raw materials for the growth of the phytoplankton.

PLANKTON PRODUCTION AND DEPTH OF WATER

The mean quantity of plankton in the surface water is greater in the shallow than in the deeper lakes. This is true of both the seepage and the drainage lakes. Very small amounts of plankton may be found at times in shallow lakes, as little as 0.26 mg/1, but no surface samples yielding as much as 3.0 mg/1 of centrifuge plankton have been obtained from drainage lakes with a depth of 9 m. or more, and none from seepage lakes with a depth of 6 m. or more.

All of the largest catches have been obtained from lakes with a maximum

depth of only 2-3 m. The relation between depth and plankton production, however, is by no means a simple one, since size, shape of basin and other factors have a modifying influence. The larger yields of the shallow lakes seem to be due largely to the fact that the raw materials required for the maximum growth of the phytoplankton may be used repeatedly because the water is so shallow that it is kept in complete circulation during the summer; thus the dissolved substances derived from decomposition and from other sources are uniformly distributed from surface to bottom and become available, therefore, for the phytoplankton.

VERTICAL DISTRIBUTION OF THE PLANKTON

Considerable variation was found in the vertical distribution of the centrifuge plankton. The mean quantity of centrifuge material in 114 series of catches, covering the entire depth of 25 lakes with a maximum depth of 18 m. or more, varied from a minimum of 0.32 mg/l in Crystal Lake to a maximum of 2.35 mg/l in Lake Mary. In these series, the largest quantity of centrifuge material was noted at the surface in 12 cases, or 10 per cent of the total number, and at the bottom in 39 cases, or 34 per cent of them; the maximum yield was found at intermediate depths in 63 series, or 56 per cent of the total number. In 43 series the maximum fell between 3 m. and 10 m., and in 20 of the 63 cases it was below 10 m. but not at the bottom.

In some series, the sample taken 1 m. above the bottom contained two to three times as much plankton as the surface sample, while in other series the surface sample yielded two to three times as much as the bottom sample. The transparency of some of these lakes is such that the phytoplankton is able to carry on photosynthesis down to a depth of 15 m. or more, so that productive growth of these forms may take place in the deeper strata in spite of the low temperature of the water at such depths. A large crop of Oscillatoria was found in the 10-15 m. stratum of Trout Lake in early August 1932 and experiments with *Coccomyxa simplex* showed that the compensation point between respiration and oxygen production fell somewhere between 10 and 15 m. in this month. Good growths of some of the aquatic mosses are found at depths of 17-20 m. in Crystal Lake.

In the various series, the maximum yield was found at a depth of 3 m. in Lake Mary on July 12, 1926, namely 4.06 mg/l of dry organic matter; this lake is small but deep so that the thermocline is near the surface; the temperature was 18.4° C. at 2 m. and 9.8° at 3 m. on the above date. The maximum production of centrifuge plankton was thus found in the thermocline of this lake. The quantity found at 3 m. was nearly two and a half times as large as that at the surface and nearly twice as large as that at 5 m. This maximum yield of centrifuge plankton at 3 m. was correlated with a crop of about 3,000 cells and colonies of phytoplankton organisms per cubic centimeter of water, but the number of these organisms was much smaller both at

the surface and at 5 m.; the number was 203 at the surface and 1,083 per cubic centimeter at 5 m., with a yield of 1.74 mg/l at the former and 2.46 mg/l at the latter depth.

CHEMICAL COMPOSITION OF CENTRIFUGE PLANKTON

From the food standpoint, the chemical composition of this plankton material is of great importance. In order to study the composition of this material, 70 samples were obtained from 56 lakes for the special chemical analyses. These analyses consisted of the determination of the organic nitrogen, the organic carbon and the ether extract. The crude protein was computed from the organic nitrogen, while the ether extract represented the fat content of the plankton. Allowing 53 per cent for the organic carbon content of the crude protein and 75 per cent for that of the ether extract, the remainder of the organic carbon was computed to carbohydrate on the basis that 45 per cent of the latter consisted of organic carbon.

The data derived from these computations showed that the crude protein content of the centrifuge plankton varied from a minimum of 0.106 mg/l to a maximum of 1.875 mg/l in the 70 samples, with a mean of 0.531 mg/l. Expressed in percentages of dry organic matter, the crude protein varied from 22 to 67 per cent, with a mean of 37 per cent. The ether extract showed a minimum of a little less than one per cent, a maximum of 13 per cent, and a mean of about 4 per cent. The carbohydrate material fell between a minimum of 29 per cent and a maximum of 81 per cent, with a mean of 59 per cent. In general then, the dry organic matter of the centrifuge plankton of the lakes of the Highland Lake District contains about 37 per cent of crude protein, 4 per cent of ether extract, and 59 per cent of carbohydrate. The ether extract was largest in those samples which contained considerable numbers of diatoms and crustacea, since both of these forms yield rather large percentages of fat.

The organic matter of the centrifuge plankton comprises a relatively small percentage of the total organic content of these lake waters; this is illustrated in Figure 2 which shows the relation between the amount of organic matter in the plankton and the total quantity found in the water of a number of lakes. Figure 4 also shows the chemical composition of the plankton of some of the lakes of this District.

COMPARISON WITH OTHER LAKES

The mean yield of 47 surface samples of centrifuge plankton from Lake Mendota, taken monthly during the year, was 1.47 mg/l of dry organic matter as compared with the summer yield of 1.36 mg/l for the surface catches of 529 lakes of the Highland Lake District. Surface catches from 23 other lakes situated in southeastern Wisconsin yielded a smaller mean

quantity of organic matter than the northeastern lakes, namely 1.11 mg/l. Comparing lakes of similar depth, the average yield of plankton in 17 northeastern drainage lakes with maximum depths of 20 m. or more, was 0.90 mg/l, while that of 12 southeastern drainage lakes of similar depth was 1.14 mg/l. Thus the amount of plankton in the surface water of the southern hard water lakes was about 25 per cent larger than that of the much softer waters of the northeastern lakes when lakes of similar depths are compared; but when lakes of all depths in the northeastern group are included, the southern hard water lakes do not show any marked advantage over the northern soft water lakes in so far as plankton production is concerned.

The total standing crop of centrifuge plankton may be computed for Trout Lake, since the area and volume are known. The lake is separated into north and south parts by a strait and the south part is rather definitely divided into an east and a west basin by a chain of islands. The east basin of the south part contains the deepest water, having a maximum depth of 35 m., and the regular station for the plankton observations is located in this part. The area of the east basin is 648 ha. and the volume is about 114,255,000 cu. m., which gives a mean depth of 17.6 m. for this part. The mean quantity of dry organic matter in the centrifuge plankton of the east basin was 0.94 mg/l, which represented a standing crop of about 166 kg. per hectare of surface. Applying similar computations to the entire lake gave a standing crop of 128 kg. per hectare. In Nebish Lake, with a maximum depth of 15.8 m. and a mean depth of 5.2 m., the standing crop of centrifuge plankton yielded an average of 61.3 kg. of dry organic matter per hectare in 8 series of observations taken during the summers from 1926 to 1932, inclusive.

In comparison with these, the hard water lakes of southeastern Wisconsin gave a much larger yield per unit of surface. The average standing crop of Lake Mendota amounted to 240 kg. per hectare, while that of Monona was 267 kg., Waubesa 241 kg., and Green Lake 250 kg. per hectare. The quantity of centrifuge plankton in these four lakes was four times as large as that of Nebish Lake and nearly twice as large as that of Trout Lake when comparisons are based upon the size of the crop per unit of area. The weight of the fresh material would be substantially ten times as large as the amounts indicated above.

FOOD AND FEEDERS

The organic content of the centrifuge plankton may be separated into food material and the organisms which feed upon it; the former consists of phytoplankton and organic débris, and the latter chiefly plankton crustacea and rotifers. In Trout Lake, the food material constitutes about 75 per cent of the dry organic matter in the centrifuge plankton, while the feeders (crustacea and rotifers) make up about 25 per cent of it.

The plankton crustacea are various and continuous feeders, so that they consume a considerable quantity of food daily. The average live weight of a Daphnia from Trout Lake, taking the various sizes as they run in a tow net catch, is 0.05 mg. and the dry weight 0.004 mg. From these weights, we may compute the amount of water that a Daphnia would have to strain in order to obtain a quantity of dry organic matter from the food material in the centrifuge plankton equivalent to its own dry weight. The centrifuge plankton of Trout Lake yielded 0.94 mg/1 of organic matter, of which about 75 per cent was food material, or 0.70 mg/1; this is equivalent to 0.0007 mg/cc of water. In order to obtain 0.004 mg. of dry organic matter then, the Daphnia would have to remove all of the food material from approximately 6 cc. of water. The weight of this quantity of water is about 120,000 times the live weight of the Daphnia. Passing such a comparatively large amount of water through its filtering apparatus is no small task for the Daphnia.

Bacteria also play a rôle in the food chain of the plankton crustacea and rotifers; as already indicated, an average of less than half of them are represented in the centrifuge material. The recent direct count method employed of Kusnetzow and Karzinkin (1931) gives a more definite idea of the abundance of the bacterial flora of lakes than could be obtained by other methods. For the past two years, the direct count method has been used by Miss Bere (1933) in making a quantitative study of the bacterial population of Wisconsin lake waters; her results show that this population is much larger than that found in previous investigations based on plate counts. Direct counts have been made on the waters of 50 lakes situated in the Highland Lake District; these determinations have covered not only the surface waters but also the various depths in several of the deeper lakes. Different types of lakes are also included in the list. The number of bacteria found in these lake waters ranged from a minimum of about 19,000 per cubic centimeter in Diamond Lake, a soft water lake belonging to the seepage type, to a maximum of 2,000,000 per cubic centimeter in Brazell or Allen Lake, which has harder water and belongs to the drainage group.

The bacterial population of Trout Lake ranged from a minimum of 32,000 to a maximum of 139,000 per cubic centimeter, with a mean of 88,000 for 11 surface samples taken between July and October in 1931 and 1932. With regard to the vertical distribution of the bacteria in Trout Lake, 124,000 per cubic centimeter were found at the surface on August 15, 1931 and 176,000 at 5 m.; the number fell to 58,000 at 10 m. and then varied from 31,000 to 54,000 in the 15-30 m. stratum. The series gave a mean of 150,000 for the epilimnion and only 48,000 per cubic centimeter for the hypolimnion. In Lake Mary, on the other hand, the number of bacteria increased with depth, rising from 358,000 at the surface to 2,000,000 at 20 m. on August 6,

1931. Nebish Lake gave a mean of 217,000 in the 0-10 m. stratum and a maximum of 759,000 at 15 m., which was 0.8 m. above the bottom.

The average number of bacteria found in the Trout Lake series taken on August 15, 1931, was 77,000 per cubic centimeter, of which about 85 per cent were rod-shaped and 15 per cent coccus forms. Using the sizes given by Birge and Juday in 1922, this number of bacteria represented a live weight of 0.104 mg/1. About 90 per cent of the live weight consists of water and 10 per cent of the dry weight represents ash; on this basis the dry organic matter of the bacteria is equivalent to about 0.0094 mg/1. Thus the dry organic material of the bacteria constitutes approximately one per cent of the amount found in the centrifuge plankton of Trout Lake.

With respect to other food sources, it seems certain that some of the material derived from disintegrating organisms reaches a stage where the centrifuge will not remove it from the water, but the plankton crustacea and rotifers are still able to filter out these colloidal particles and use them for food. Under the classification adopted for this report, these particles belong to the non-centrifugible material.

SUMMARY

1. The quantity of dry organic matter in the centrifuge plankton of the surface waters of 529 lakes varied from 0.23 to 12.0 mg/1, with a mean of 1.36 mg/1.

2. The seasonal and annual variations in the amount of dry organic matter in the centrifuge plankton ranged from none to eightfold.

3. The surface waters of the drainage lakes yielded larger amounts of centrifuge plankton than those of the seepage lakes; the mean quantity of dry organic matter in the former was 1.58 mg/1 and in the latter 1.09 mg/1.

4. The organic matter in the centrifuge plankton consisted of 37 per cent crude protein, 4 per cent ether extract and 59 per cent carbohydrate.

5. The northern soft water lakes yielded a smaller amount of centrifuge plankton per unit of surface than the southern hard water lakes.

PART II

THE NON-CENTRIFUGIBLE ORGANIC CONTENT OF THE WATER

By E. A. BIRGE

The organic content of the water of any lake must be considered primarily as a unit of composition and of action. We analyse this unit into parts by mechanical and chemical processes in order to make a beginning of understanding both its numerous constituents and the intricacy of their actions and reactions with each other and with their environment.

It is, therefore, convenient to consider first the total organic content of the water, including plankton. This content our chemical processes have

analysed into three organic constituents, crude protein, ether extract or fat, and carbohydrate. Mechanical analysis separates *plankton*, or particulate organic material, from that which, for brevity's sake, is called *dissolved*. It is recognized that both words, plankton and dissolved, are used rather for convenience than with scientific accuracy.

For the study of the organic matter the residues remaining from the evaporated water of the lakes have been analysed in the same way as the plankton and the same methods of computation have been employed. Organic carbon, organic nitrogen, and ether extract have been determined, and from these determinations the three organic constituents of the residues have been computed—the crude protein, the ether extract and the carbohydrate. These are regarded as a first approximation to the determination of the constituents of the organic content of the water. They serve as a beginning of knowledge of that organic complex and as a basis for more detailed studies.

In computing the organic matter of the residues from these determinations we have assumed the following percentages of carbon in the three organic constituents: crude protein, 53 per cent; fat, 75 per cent; carbohydrate, 45 per cent. The first two figures call for no comment, the third needs explanation. The estimate of 45 per cent is based on the fact that the numerous non-nitrogenous substances of the residues are mainly solutes of one sort or other.

Recently, numerous analyses have been made to determine the amount of lignin-like substances present in muds, residues, etc., as found in lakes. The results of some 50 analyses by the methoxyl method show that the indicated amount of lignin is very variable; that the mean amount is small, about 9 per cent of total organic and less than 12 per cent of the non-nitrogenous matter. This method of analysis is the only one at present applicable to the small quantities of residue available for analysis; its results are satisfactory when applied to wood; but it is by no means certain that they are equally reliable when applied to a complex mixture of organic substances like that found in residues. This being the situation, we still retain the estimate of 45 per cent, although this estimate was first used for plankton and was based on the assumption that most of the carbohydrates of plankton are of the cellulose type. This is by no means certain or, perhaps, even probable for the residues; but we have not thought it wise to make any change without more careful study.

THE ORGANIC ANALYSES

In the course of this investigation there have been evaporated more than 1900 samples of water from 529 lakes of the District. The dry residues weighed from 10 mg/l to 110 mg/l; with a mean value of 43 mg/l. This weight is much smaller than that of similar residues from the hardwater lakes of southern Wisconsin, whose waters contain, as a mean value, residues weighing about 200 mg/l. In general, no great changes in the amount of residues are correlated with the depth from which they come. Ordinarily

the residues near the bottom are somewhat greater than those at the surface. In our studies we endeavored to obtain the bottom sample of water from a depth about one meter above the bottom, in order to avoid the large amounts of organic débris which are likely to be found at depths nearer the mud. In Trout Lake 25 pairs of samples from surface and bottom (30 or more meters) gave a mean of 57.8 mg/1 for the surface and 64.2 mg/1 for the bottom. This is a fair example of the ordinary situation.

The percentage of organic matter in these residues is very variable, as is shown in Table 1. It is greatest in lakes of the bog type, whose water gains much extractive organic matter and little inorganic matter from the environment. In such lakes the organic matter may be more than 80 per cent of the total residues, with a weight of residue as great as 60 mg/1, though usually from 20 to 35 mg/1. In such lakes the inorganic matter may be as little as 4.5 to 6.5 mg/1, quantities quite as small as are found in any of the lakes. In lakes with clear water which contains the minimum amount of residue—from 10 to 18 mg/1—the percentage of organic matter rarely falls below 20 per cent and may be as great as 35 per cent. The smallest percentages are found in deep lakes whose water has relatively large inorganic content and small organic content. The surface residues of Trout Lake are 57.8 mg/1; the organic matter is 8.07 mg/1, or 13.8 per cent. This is a fair sample of such lakes. The minimum percentage of organic matter in such lakes is 10 per cent and the maximum does not exceed 20 per cent.

In the hard-water lakes of southern Wisconsin, the organic content may be less than that of Trout Lake; but its usual range is from amounts about as large as that of Trout Lake to those that are twice as great. Since the total residue is nearly or quite 200 mg/1 the percentage of organic is correspondingly small.

ORGANIC CARBON

The most important determination of organic matter is that of the carbon. This element contributes nearly 50 per cent of the organic matter contained in the water and the ratio is not very variable. As computed by our method the total organic is not smaller than 2.1 times the carbon and it is always less than 2.2 times the carbon. The exact value depends on the distribution of the three primary constituents of the organic matter. For general purposes little error is made if the value of total organic matter is stated as twice that of the organic carbon.

It is necessary to classify the large number of lakes which we have examined in order to get our knowledge into a form capable of intelligent discussion. We make two primary groups of the lakes of the Highland Lake District; *seepage lakes,* or lakes without an outlet, and *drainage lakes,* which are connected with the regular drainage system of the region. As is usual in such classification, there are a few lakes which might be put into either of the

groups; but we enumerate 238 seepage lakes and 291 drainage lakes. Both groups are subdivided according to the amount of organic carbon found in their water. We assign a group for each milligram of carbon per liter of water up to 20 mg/1. The 13 lakes whose carbon exceeds 20 mg/1 are classified into two groups—20.0-22.9 mg/1 and 23.0-28.5 mg/1 respectively. For most of the purposes of this paper the differences between seepage and drainage lakes do not enter into the story, and the classification by carbons is of chief importance. This method of classification is especially satisfactory since the amount of organic carbon in any lake is usually fairly constant, both when considered with relation to depth or to time.

Organic carbon ranges from 1.15 mg/1 to 28.5 mg/1. The minimum amounts are found in clear, deep seepage lakes whose water has little inorganic matter, so that total residues are 10-12 mg/1. The largest amounts are found in lakes of two types; first, shallow and active lakes (1 to 3 m. deep) with large growths of plankton; second, lakes, mostly of a deeper type (6 to 9 m.) with little plankton and great amounts of extractive carbon from marsh or peat. The mean amount for all lakes is 7.65 mg/1; but this is very unevenly divided between the two types of lakes. The mean amount of carbon in drainage lakes is little less than twice as great as that in seepage lakes; the numbers are 9.79 mg/1 for drainage lakes and 5.05 mg/1 for seepage lakes; the ratio is 100 to 51.6.

There are 57 seepage lakes, little less than 25 per cent of the whole number, whose organic carbon is less than 3 mg/1; only 3 drainage lakes have so little. Of these three lakes one is rather a large spring than a normal lake and in the other two cases the carbon is so near to 3 mg/1 that a larger number of samples of water would probably give results greater than 3 mg/1. On the other side, only 2 seepage lakes have carbon exceeding 20 mg/1, while 11 drainage lakes have so much. In only 2 seepage lakes does C = 15.0-19.9 mg/1, while 31 drainage lakes are so classified. In only 6.7 per cent of seepage lakes does the water contain 10 mg/1 or more of carbon; while 43.3 per cent of drainage lakes are in that class. The amount of total organic matter closely follows that of the carbon; so that it is evident that a unit-volume of water in an average drainage lake contains about twice as much food, actual and potential, as does a similar unit in a seepage lake.

ORGANIC NITROGEN

The range of organic nitrogen is from 0.108 mg/1 to 1.920 mg/1; the mean value for 529 lakes is 0.457 mg/1. The relation between seepage and drainage lakes in regard to nitrogen is much the same as that for carbon; the figures are: drainage lakes, 0.559, seepage lakes, 0.331 mg/1; a ratio of 100 to 57.3. This difference, however, is primarily a function of the amount of total organic matter in the two types of lakes; and it does not imply a cor-

responding difference in the two types where the total quantity of organic is similar. The carbon-nitrogen ratio is much the same for the two types where the amount of carbon is similar. Thus 157 seepage lakes in which C = 1.0-4.9 mg/1 have a mean C/N ratio of 12.9 while in 51 drainage lakes of the same group the ratio is 12.5.

The range in quantity of nitrogen from the minimum of single cases to the maximum is of the same order as that of carbon; but the statement does not hold when limiting groups of lakes are considered, rather than single instances. There are 14 lakes in which C = 1.0-1.9 mg/1; the mean value of their carbon is 1.74 mg/1 and that of nitrogen is 0.157 mg/1. There are also 13 lakes in which C = 20.0-25.9 mg/1; their mean carbon is 23.13 mg/1 and nitrogen 0.903 mg/1. Thus the carbon of the maximum group is 13.3 times that of the minimum; while nitrogen has increased only 5.7 times, or less than half as much.

The result of this situation is that the percentage of crude protein becomes smaller as the quantity of total organic becomes larger. In the minimum group named above C/N = 11.1 and in the maximum group the ratio is 27.8.

ETHER EXTRACT

We employ the term *ether extract* rather than *fat* in recognition of the fact that ether may extract small quantities of other material than fat, such as chlorophyll; and that other solvents may be able to extract more fat from the residues than can be removed by ether. We have followed a standard method and report results in terms of the method. There is no doubt that the ether extract practically represents the fats of the residues.

Ether extract is the smallest constituent of the total organic matter and it is the most irregular in its distribution. We have made more than 500 determinations of ether extract and in only two did the quantity reach or exceed 0.500 mg/1; we believe, however, that larger amounts may be found occasionally, though rarely, in lakes of the District. The mean value for all cases is 0.156 mg/1; the smallest mean is found in 29 cases where C = 1.0-1.9 mg/1; in this group ether extract is 0.093 mg/1 and 2.69 per cent of the total organic. In the group where C = 4.0-4.9 mg/1 ether extract has risen to 0.183 mg/1, or 1.93 per cent of total organic. From this value of carbon on there is no definite increase of ether extract; the mean of 135 cases where C = 5.0-9.9 mg/1 is 0.187 mg/1, but it is lower in groups with more carbon. Ether extract for 141 cases where C = 10.0 mg/1 or more is 0.163 mg/1.

When residues are distributed by quantity of carbon, each group representing one mg/1, the range of ether extract in each group will be found to be nearly or quite ten-fold as compared with a three-fold range in the amount of nitrogen. The result is to render the means of ether extract for the several groups very uneven as compared with those of crude protein.

Since the quantity of ether extract does not rise with that of total organic its percentage necessarily declines as total organic increases. Lakes whose carbon is 1.0-1.9 mg/1 have about 3.71 mg/1 of total organic and 2.69 per cent of ether extract; where C = 20.0 mg/1 or more total organic is 50.34 mg/1 and the per cent of ether extract has become 0.32, or little more than one-ninth of the first named figure.

TOTAL ORGANIC CONTENT INCLUDING PLANKTON

Examples of the results of our analyses of residues from the waters of lakes in northern Wisconsin are shown in two sets of diagrams. Figure 2 shows these facts for a series of 15 typical lakes. The diagrams give the quantity of organic matter found in the water; the quantity of its three primary constituents; and the amount of centrifuge plankton. The percentile diagrams show the percentages of each of these constituents and of the plankton. Other data for these lakes are given in Table I. Figure 3 shows, in a more general form, the same facts for a series of groups of lakes, that have been classified on the basis of quantity of organic carbon.

TABLE I. Data regarding lakes whose organic content is shown in Figure 2.

Lake	Type	Area, ha.	Depth, m.	Res. mg/1	Org. mg/1	Per Cent	Color
Diamond	S	48	12.2	12.6	3.26	25.9	0
Pauto	S	10	17.2	12.4	4.45	35.9	0
Hillis	S	5.2	9.0	22.7	7.36	32.4	0
Trout	D	1051	35.0	59.4	7.96	13.4	3
Black Oak	D	230	26.0	35.0	8.51	24.3	8
Finley	S	63	8.5	22.3	10.19	45.7	8
Bragonier	S	19	8.7	24.7	13.33	54.2	29
Adelaide	D	22	21.0	34.7	15.90	45.8	37
Crab	D	345	18.0	42.6	22.15	51.9	44
Little Long	D	15	18.0	51.6	29.15	57.2	132
Yolanda	D	1.9	7.5	43.0	33.59	77.9	146
Mary	D	1.2	22.5	57.4	37.58	65.5	113
Kate Pier	D	39	4.0	82.9	44.55	53.7	220
Brazell	D	16	2.0	102.0	55.15	54.1	250
Helmet	S	14	8.5	71.5	55.34	77.4	268

NOTES: *Type:* S = seepage lake or lake having no outlet. D = drainage lake.

Area. The area for Trout Lake is that of the part lying south of the strait connecting the two parts of the lake.

Depth. These are maximum depths. Most of the lakes are simple basins; but Trout Lake is divided by a subaqueous ridge which rises into small islands. Crab Lake is a shallow body of water with numerous islands and bays. Deep water is but a small part of the area.

Residue. The figures are somewhat below the fact, since part of the carbonates is hydrolysed in evaporation. Trout Lake is probably the only case where appreciable error is caused; in that lake total organic would be about 11 per cent instead of 13, if there were no hydrolysis.

Color. The colors are stated on the scale of the U. S. Geological Survey, the platinum-cobalt scale.

Table I gives the more important facts regarding the lakes whose organic content is shown in Figure 2. Six of the lakes have no outlet and are called seepage lakes; nine of them have outlets, but Adelaide, Mary, and Yolanda lakes overflow only in spring or in rainy seasons. Kate Pier and Brazell

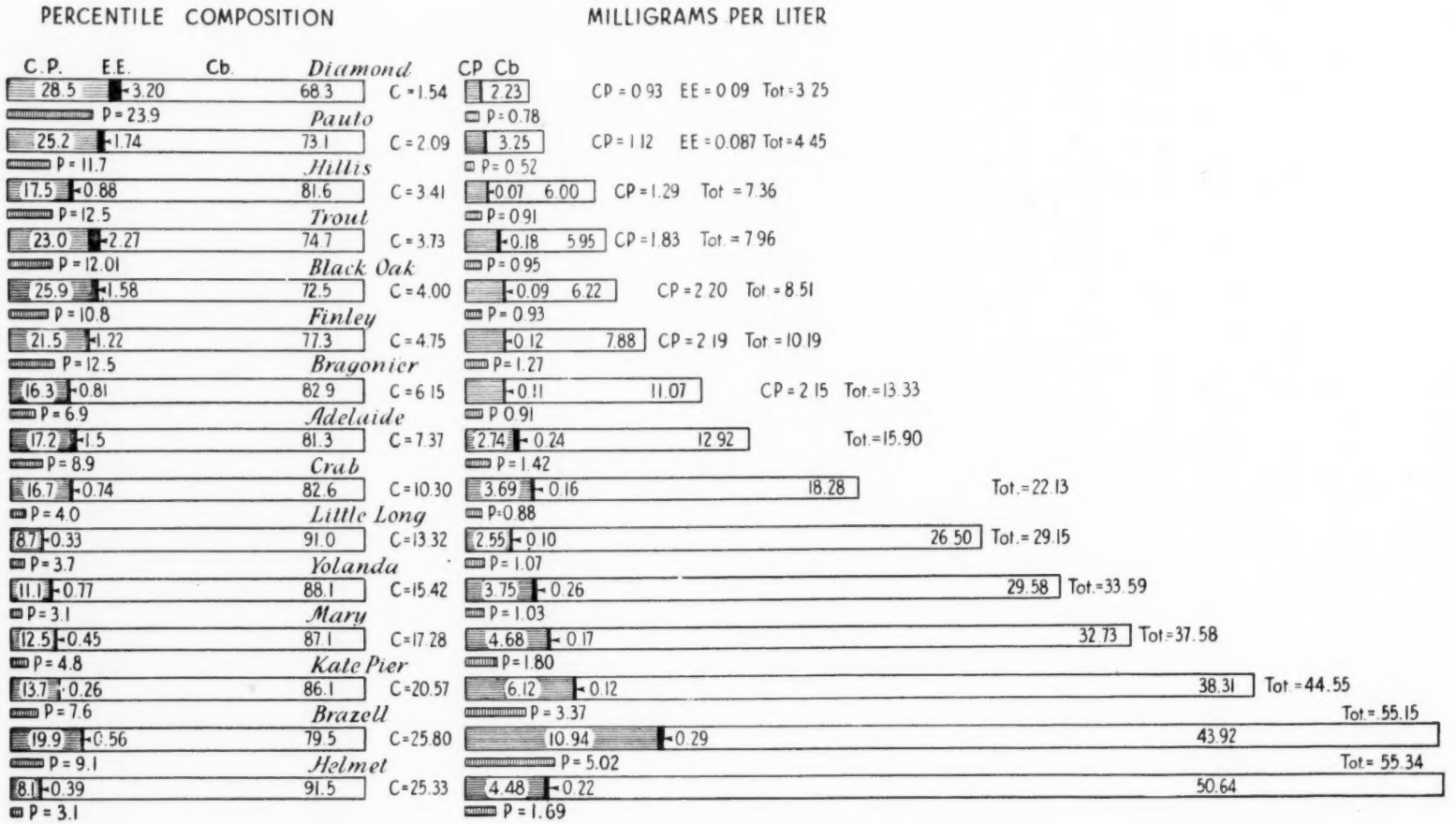

FIG. 2. Quantity and composition of organic content of a series of lakes. C, organic carbon; Cb, carbohydrates; C.P., crude protein; E.E., ether extract or fat; P., plankton; all quantities stated as mg/l. For further data on these lakes see Table I.

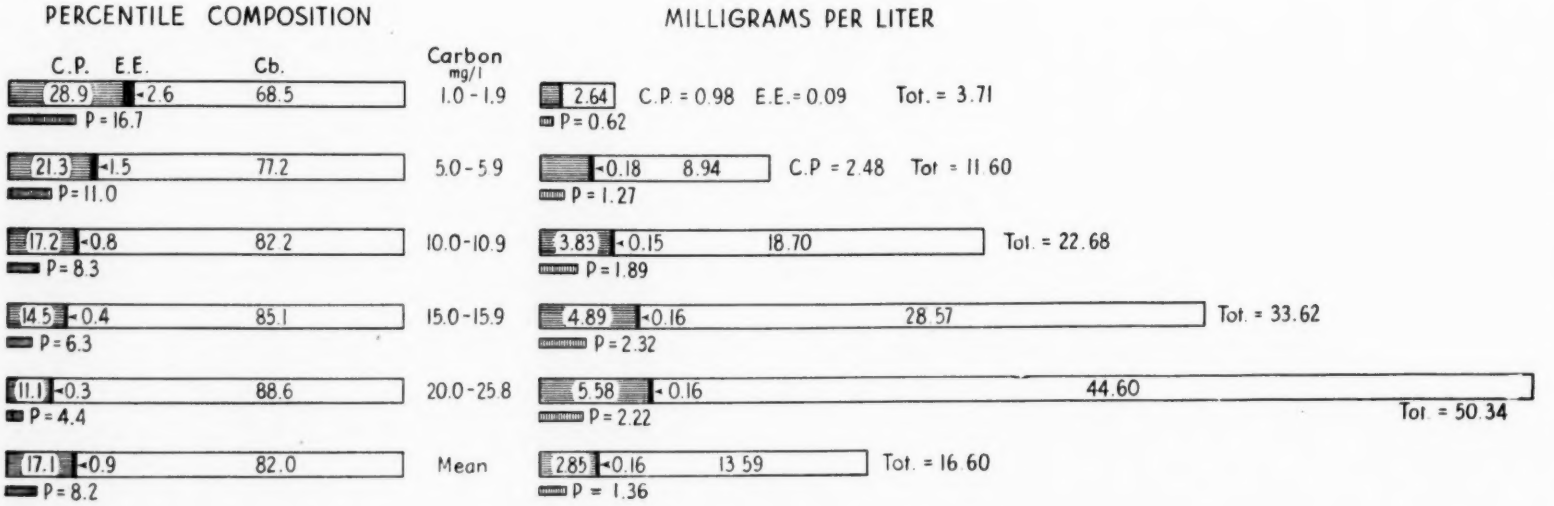

FIG. 3. Mean composition of organic content of certain groups of lakes, classified by amount of organic carbon. Letters as in Figure 2. The final mean result is derived from all groups of lakes, as thus classified, each group being given a weight corresponding to the number of lakes in it. Mean percentages are computed from mean quantities thus ascertained.

lakes are shallow lakes lying in the course of streams carrying much inorganic matter; their water is continually renewed from this source. Trout and Crab lakes have several tributaries and their outlets are streams of fair size for the District.

Surveys have been made of 11 of these lakes and the facts of their organic matter are based on samples from all depths and are computed with reference to the volume of the water; such surveys have not been made of Crab, Kate Pier, Brazell, and Helmet lakes, and the results are based on residues from the surface water. This fact makes little difference, since the organic matter is distributed through all depths of these lakes in a fairly uniform manner. In Trout Lake, for instance, the total organic matter, computed from surface samples only is 8.07 mg/l; computed from residues from all depths its value is 7.96 mg/l.

These lakes have been selected to represent the range of values of organic matter, both in quantity and in composition, as influenced by the nature of the lake. A result of this method of selection is that the series of colors of the water is not an even one, although it covers the full range of color found in the District.

Figures 2 and 3 show substantially the same class of facts; the quantity of organic matter in the lakes of the Highland District, its composition both in quantity and percentage. In both cases the arrangement is based on the quantity of organic carbon found in the water, since the amount of organic matter depends upon the carbon and since the carbon is determined directly by chemical analysis and without computation. Figure 2 illustrates the kind of individual variation which the lakes may present and Figure 3 shows the effect of averaging the results from groups of lakes that agree in amount of organic carbon.

These two diagrams may be treated together and it is well to consider first the total organic content of the water, including plankton, and later to consider the different elements from which the total is derived.

Every diagram of these figures emphasizes two primary facts; first, that the water of small fresh water lakes contains relatively large amounts of organic matter; second, that formed organic matter, as represented in the plankton, constitutes only a small fraction of total organic matter. In the plankton are found the organisms which are the chief agents of the lake for the internal manufacture of organic matter; yet these, together with the mass of particulate but unformed organic matter that accompanies them are far less in quantity than is the dissolved organic matter derived primarily from them.

The diagrams show a series of waters, extending from those in which plankton and its derivatives constitute the total organic to those in which they are only a small addition to organic matter derived from the environ-

ment. We are not surprised to find large amounts of organic matter in lakes whose water is deeply stained by extractives from marsh, or to discover that in such lakes the plankton is only a small part of the organic content; but there is a surprisingly large amount of dissolved organic matter in lakes which manufacture all but a minimum part of their organic content. In such lakes the plankton is the primary source of five to six times its own weight of organic solutes.

These diagrams represent conditions in small inland lakes; but these conditions are found, so far as is known, in all bodies of fresh water. The larger inland lakes, such as Seneca Lake, the Great Lakes, like Erie and Superior, tropical lakes and those near the Arctic circle, all furnish results which may easily be fitted into this series of diagrams.

Compare first the lakes which open and close the series in Figure 2, Diamond and Helmet lakes. Both are seepage lakes, having no outlet and deriving their water from rain that falls on the lake and on its immediate environment. As a result the water contains little inorganic matter, 9.3 mg/l in Diamond Lake and 16 mg/l in Helmet Lake. The hydrogen ion is the same for both lakes, pH 5.7. Organic matter differs enormously, chiefly because the water coming to Diamond Lake from the ground passes through a sand filter, while that which enters Helmet Lake comes through peat beds. The main result is to give Helmet Lake a content of organic matter nearly 17 times as great as that of Diamond. Equally conspicuous is the difference in composition of the organic matter. The extractive matter from peat consists in large degree of carbohydrate with only small percentages of crude protein and of ether extract. This fact is conspicuous in the diagrams. Crude protein in Diamond Lake is 0.93 mg/l and in Helmet Lake it is 4.48 mg/l; an increase less than five-fold. Carbohydrate in the two lakes is 2.23 mg/l and 50.64 mg/l respectively; having increased nearly 22 times. Ether extract is, as everywhere, a very small quantity, almost negligible in these lakes. Diamond Lake has 0.09 mg/l of this and Helmet has 0.22, little more than twice as much. These differences are reflected in the diagrams showing percentile composition. In Diamond Lake crude protein is at a maximum, 28.5 per cent; in Helmet there is only 8.1 per cent. The percentile decline is even greater in ether extract, from 3.2 per cent to 0.39 per cent. Carbohydrate rises from about two-thirds in Diamond Lake (68.3 per cent) to more than nine-tenths in Helmet Lake (91.5 per cent).

The plankton shows a situation much like that of the protein or the ether extract; the quantity in Helmet Lake is hardly more than twice as much as in Diamond (0.78 and 1.69 mg/l), with a consequent reduction of per cent from 23.9 to 3.1.

Thus Diamond Lake offers an extreme case of lakes whose organic con

tent is derived primarily from the plankton growing in the lake and Helmet Lake is an equally extreme example of lakes whose organic content is chiefly composed of extractives from the environment. The numerous lakes of the District lie between these extremes. Their organic content depends, both in quantity and composition, on these two primary factors; but there is an infinite variety in detail, dependent on the inorganic content of the water and on the nature of the environment. Some part of this variety is illustrated by the series of lakes in Figure 2.

The first two lakes of Figure 2, Diamond and Pauto, are of the same type. They are seepage lakes with very clear water; the quantity of dry residue is small and is about the same in both lakes. In Pauto Lake the amount of organic matter is greater than in Diamond, and the percentage of crude protein, ether extract, and plankton are less than those of the first lake. The lake is much smaller than Diamond and the volume of water in contact with the bottom is therefore correspondingly less. We therefore think, though there is no direct evidence, that organic matter extracted from the bottom mud is responsible for the difference in composition of the organic content. Much of the organic matter of this ooze is derived from the plankton of the overlying water.

Four cases represent lakes with 3 and 4 mg/1 of carbon; in these two groups are found 148 of the 529 lakes of the District which have been examined. Two of these lakes, Trout and Black Oak, represent the large and deep lakes; Trout Lake being the deepest of the District. These have a relatively low percentage of organic content in their residue; this is especially marked in Trout Lake, because of the large content of inorganic matter. The other two lakes in this group, Hillis and Finley, are seepage lakes, fairly representative of such lakes with 3 and 4 mg/1 of carbon. Hillis Lake has less protein than is common in such lakes. Every group of lakes with less than 6 mg/1 of carbon has protein at a mean value of more than 20 per cent. The percentile value of plankton in all four lakes is much the same and is about that of the groups to which they belong.

The next three lakes, Bragonier, Adelaide, and Crab, represent middle values in quantity and in composition of organic matter, and the same is true for color, as is seen in Table I. The percentage of both protein and plankton falls off greatly as compared with that in groups with smaller amounts of organic carbon. The protein of these lakes is fairly characteristic of the groups represented, but the plankton is smaller than their average.

The six lakes which close Table I are taken from groups with much carbon and high color. Their carbon ranges from 13 mg/1 to 20 mg/1 and above; in all cases the color is more than 100 and in three cases it exceeds 200. Both facts indicate much extractive organic matter. There is, however, much difference between these lakes. Two of them, Little Long and Helmet, represent extreme cases of extractives from marsh; Little Long Lake being

at a lower quantitative level than Helmet; but the two lakes agree almost exactly in percentile composition of organic matter, and in percentage of plankton. The difference in quantity is reflected in the lower color of Little Long Lake.

The contrast between Brazell Lake and Helmet is equally instructive. Here are two lakes in close agreement so far as concerns color of water and quantity of organic matter, but differing widely in its quantitative and percentile composition and in plankton. Brazell Lake lies in the course of a stream; it is in a region of cultivated ground; it is very shallow, so that all the water is thoroughly warmed to the bottom, and the organic ooze is filled with life and active decomposition. The result is an exceptionally large amount of protein and of plankton. On one occasion the organic matter in the plankton of this lake was almost 12 mg/1; the largest amount found in any lake of the District. Helmet Lake is the reverse of Brazell in all of these qualities; it is relatively deep; its organic matter is of a type not readily decomposable; the temperature of the bottom water rarely exceeds 6° C. The results of all of these facts are indicated in the diagrams. Kate Pier Lake is of the same type as Brazell, on a lower scale of quantities, and holds a relation to it similar to that existing between Little Long and Helmet. Similar lakes may be found with organic carbon that covers a wide range of values; there seem to be none with less than 5 mg/1.

The diagrams of Figure 3 are selected from those furnished by the lakes when classified into groups characterized by content of organic carbon. They show in more general form the same facts as do the individual lakes. In diagrams showing quantity the mean amount of organic carbon increases from 1.74 mg/1 in the minimum group to 23.13 in the maximum group; a ratio of 1:13.2. Total organic rises from 3.71 mg/1 to 50.34, mainly through the increase of carbohydrate. The maximum protein is 5.7 times the minimum; while carbohydrate rises to nearly 17 times the minimum, or roughly three times as much. Fats, represented by ether extract, are little more than a negligible quantity at best; where C = 5.0-5.9 mg/1 they are twice as great as where C = 1.0-1.9 mg/1, but there is no further rise. The quantity of plankton doubles in the same groups, but it does not double again in the course of the series. The percentages reflect these facts, much as they do in Figure 2.

The mean values given are weighted for the number of lakes in the 21 groups into which the lakes are classified by their carbon content. This mean therefore represents the situation in the "average lake" of the District. The mean percentages are computed from the mean quantities thus obtained. There is a noteworthy correspondence between these percentages and those given for the group whose C = 10.0-10.9 mg/1. For other purposes, other and different means may be computed from the data. If the mean of the

several groups is taken without weighting for the number of lakes, the total organic will be 25.1 mg/1, with corresponding changes in percentile composition.

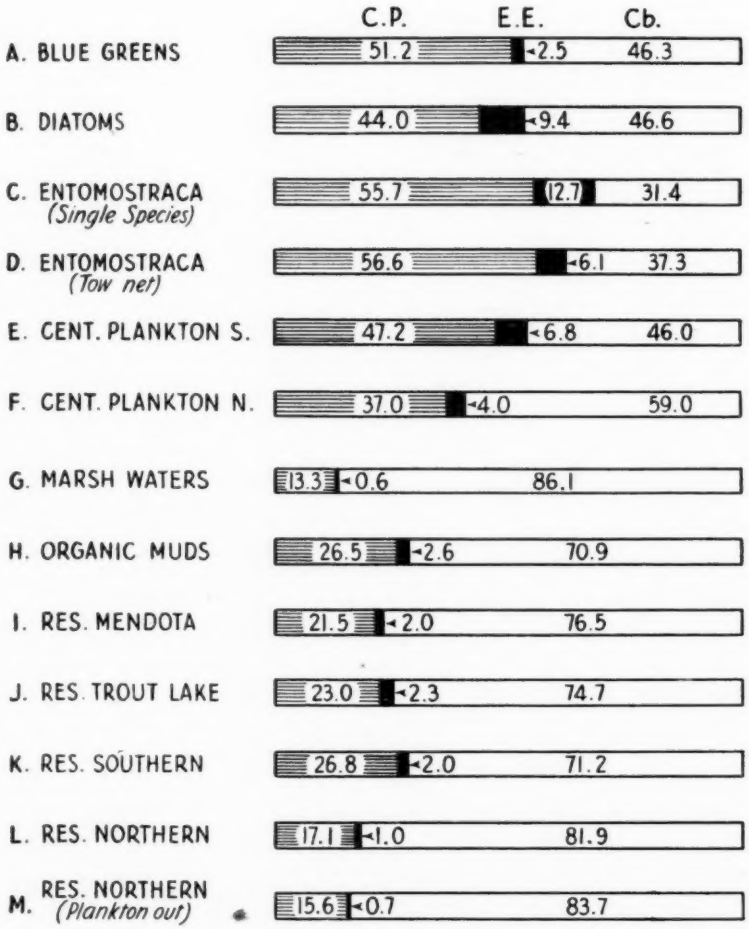

Fig. 4. Mean percentile composition of organic matter from various sources in lakes. A, 22 analyses of blue-green algae; B, 16 analyses of diatoms, all from lakes of southern Wisconsin; C, 36 analyses of single species of entomostraca, 6 Copepoda, 16 Daphnia, 12 Holopedium, 2 Leptodora; D, 40 analyses of mixed entomostraca, tow-net catches from northern lakes; E, 124 analyses of plankton from southern lakes, from Birge and Juday, Plankton Report, 1922; F, 70 analyses of centrifuge plankton from northern lakes; G, 41 analyses of waters from northern marshes; H, 66 analyses of organic content of muds from northern lakes; I, 60 analyses of organic content of residues from Lake Mendota; J, analyses of 14 series of residues from Trout Lake, 7 samples in each series; K, mean results from 24 southern lakes; L, mean results from 529 northern lakes, obtained as stated under Figure 3; M, same mean as corrected for removal of plankton; composition of plankton as shown in diagram F, above.

In most of these diagrams, the inclusion of more analyses would probably modify percentages.

SOURCES OF THE ORGANIC MATTER OF THE RESIDUES

In Figure 4 are given 13 diagrams representing the percentile composition of the organic matter contained in various residues and of the sources from which this organic matter is derived. For comparison there are also included diagrams showing composition of similar substances from the hard-water lakes of southern Wisconsin.

The diagrams of central importance are F, G, and H, which show the mean percentile composition of the organic matter of centrifuge plankton, of organic matter from marsh waters, and from the upper strata of the bottom muds. These are the main sources of the dissolved organic matter, whose mean composition is shown in diagram L, which is repeated from the mean of Figure 4. Diagram M shows this mean composition after deducting plankton and adjusting percentages according to the data of diagram F; it represents the mean result given in Table II, p. ???.

Diagrams A-D give the mean percentile composition of organisms from which plankton is derived. The algae analysed came from lakes of both northern and southern Wisconsin; the same is true of the analyses of single species of entomostraca. Diatoms were from southern lakes, no catch of pure diatoms having been made in the north. The tow-net crustacea, the residues from marsh waters, and the bottom muds are all from the Highland Lake District.

Numbers E, I, and K present results from southern waters for comparison with those from the north. Diagram I, the composition of residues from Lake Mendota, is to be compared with J, that of Trout Lake. Each of these lakes has furnished a much larger number of analyses than any other lake of its district. These three diagrams are intended to show the characteristic resemblances and differences between the hard-water lakes of southern Wisconsin and the soft-water lakes of the north, which are the main subject of our study. This comparison will now be briefly stated.

COMPOSITION OF ORGANIC CONTENT OF WATERS OF LAKES FROM NORTHERN AND SOUTHERN WISCONSIN

The diagrams of percentile composition of organic matter from lakes of southern Wisconsin are inserted in order to show the essential agreement of such material from hard-water and soft-water lakes; and also to bring out the characteristic differences. The composition assigned to plankton is that reported from Mendota, Monona, and Waubesa lakes in the Plankton Report of Birge and Juday (1922). The samples were collected in 1915-17. These lakes have much larger growths of algae than appear in the northern lakes and this fact is reflected in the higher percentage of crude protein. They have also large growths of diatoms, especially in spring and autumn, such as rarely appear in the north. To this fact is due most of the difference in percentage of ether extract in the plankton.

The diagram of the composition of organic residues from Lake Mendota is based on 60 analyses from 103 samples taken at fairly regular intervals during 1926-31. Work on this collection is not yet complete, but it is plain that no great difference is likely to appear between the situation in Mendota and that of Trout Lake. The quantity of organic matter in Mendota is 14.1 mg/l, as compared with 8 mg/l in Trout Lake.

In the mean results from 24 southern lakes, each lake appears by its mean results, not by the single samples. None of these southern lakes have high-colored water, due to extractives from marsh, with correspondingly large amounts of organic carbon. In only two cases out of fifty-five did the organic carbon exceed 10 mg/l. The larger percentage of crude protein in these lakes is partly due to this fact and partly to the larger growths of algae and crustacea in these lakes, whose higher inorganic content encourages such developments.

COMPOSITION AND SOURCES OF ORGANIC CONTENT OF LAKES OF THE HIGHLAND LAKE DISTRICT

In the series of diagrams representing the composition of various elements of the organic content of these lakes, none is found for the higher plants, those growing from the bottom of the lake. The omission is intentional, since additions from this source to the organic content of the water may be neglected. These plants contain only a small amount of organic matter, relatively to the total volume of water in the lake. This is especially the case in northern lakes, few of which have large weed beds. Moreover, such plants, as they die, fall to the bottom, where they accumulate and their organic matter returns to the water, in small part by direct solution from the lake mud, but chiefly in the form of lower products of decomposition.

Primary attention should be given to the percentages of crude protein in following the series of diagrams in Figure 4 from those showing composition of living organisms to those showing the dissolved organic content of the water. The general facts for ether extract are much the same as those for protein; but the amount and the percentage of ether extract are small and variable, both in the mean results and in the analyses from which these are derived. Protein is present in such large amounts that its changes are significant and can be estimated with fair accuracy.

ORGANISMS AND PLANKTON

Compare first the percentage of protein in the centrifuge plankton with that of the plants and animals which are its primary source. The mean value of crude protein in both algae and entomostraca is more than 50 per cent; the protein content of plankton from northern lakes is 37 per cent, or from one-third to one-half less than that of the organisms.

This situation is not the result of certain exceptional values, raising the

mean percentage of protein in the algae and lowering that in plankton. On the contrary, there is only one analysis of algae in which crude protein is less than 40 per cent; 10 are between 40 and 49 per cent; and 13 are above 50 per cent. There are only about 10 per cent of all the analyses of crustacea in which protein is less than 50 per cent. On the other hand out of 70 analyses of plankton only five are found whose protein is 50 per cent or more; in the other 65 cases, the percentages of 22 are in the 20's, those of 25 are in the 30's and there are 19 in the 40's.

Still more significant is the situation shown by analyses of plankton from lakes whose relative content of plankton is large and whose extractive organic matter is very small. There are analyses of plankton from 13 such lakes; their mean carbon content is 3.44 mg/l; color of the water is 4.4; plankton is 14.4 per cent of total organic, or about one-sixth of the dissolved organic matter. The value of the protein in this plankton is 30 per cent or 7 per cent below the mean percentage in all analyses of plankton.

Thus in the making of centrifuge plankton out of living organisms and their immediate derivatives, the protein content of such organisms disappears more rapidly than does carbohydrate until an approximate equilibrium of composition is established at a lower level of nitrogenous content. This loss of protein takes place partly by chemical processes of rapid decomposition, and partly mechanically, by the sinking of plankton organisms to the bottom of the lake.

During the summer, at least, the supply of new organic matter to the plankton from the organisms approximately equals the loss by decomposition and settling; and both the amount and the percentile composition of the plankton in any lake remain fairly constant. The same may also be said of the plankton in groups of lakes that are of the same type.

PLANKTON AND DISSOLVED ORGANIC MATTER

The passage of organic material from centrifugible plankton to uncentrifugible dissolved matter must be considered first in the light of those cases in which plankton is the primary source of the dissolved material; or, at least, the only source that can be definitely recognized. But first a table should be given, modifying the data used in Figure 3 by subtracting the plankton and readjusting the percentile composition of the several groups according to the mean composition of the plankton, as given in Figure 4.

Table II, taken in connection with Table I and Figures 2 and 3, indicates at once the fact that the content of lake water in dissolved organic matter comes from two kinds of sources, those internal to the lake and those external to it. Plankton and lake bottom are sources of the first type and extractives from marsh and peat represent the second.

TABLE II. Quantity and Percentile Composition of Total Organic Matter, after Subtracting Plankton.

Carbon, mg/1	Total Organic mg/1		Percentile Composition			Diss. Org. / Pkn.
	Plankton	Dissolved	C. P.	E. E.	Cb.	
1.0– 1.9	0.62	3.09	24.3	2.3	73.4	5.0
5.0– 5.9	1.27	10.33	19.4	1.3	79.0	8.1
10.0–10.9	1.89	20.48	14.4	0.4	85.2	10.8
15.0–15.9	2.32	31.30	12.9	0.2	86.9	16.5
20.0–25.8	2.22	48.12	9.9	0.2	89.9	21.7
Mean	1.36	15.24	15.6	0.7	83.7	11.2

NOTE: The data in this table should be compared with those given in Figure 3.

ORGANIC CONTENT OF MUDS AND DISSOLVED ORGANIC

There is little to say regarding solutes originating in the mud of the lake, since no considerable study has been made of them. Their quantity seems to be small in what may be called a normal lake. It will be seen later that such a lake may have about six times as much organic matter in the form of solutes as in the plankton. In Lake Michigan the dissolved organic was found to be 7.22 mg/1 and plankton 1.22 mg/1; a ratio practically identical with that of numerous small inland lakes with exceptionally clear water. External sources must furnish only a minimum amount of organic material to a lake of the type of Michigan and the results of solution from the bottom must be negligible. Less trustworthy observations, because older ones, on Seneca and Cayuga Lakes, N. Y., lead to about the same ratio of plankton and organic solutes.

There is, however, a type of lakes found in the Highland Lake District whose water has much more organic carbon than would be inferred from the color of the water. Among the lakes whose carbon is 10 mg/1 or more there are 12 whose color is about half that of the other lakes in the carbon group to which they belong, or in some cases much less than half. These lakes are of the same type in other respects; they are shallow and have abundant plankton; most of them lie in the course of a stream. Such lakes have exceptional opportunities for securing organic solutes from the bottom and we have supposed that the low color of their organic matter was associated with its origin from that source. Definite proof is, however, still lacking.

In other lakes whose shallow waters pass almost insensibly into boggy margins, much of the distinction vanishes between external and internal sources of this kind. In any normal lake, as distinguished from a bog lake, the plankton is the main source of the organic matter found on the bottom; so that much of the contributions from the bottom originate indirectly from plankton.

QUANTITATIVE RELATION OF PLANKTON AND SOLUTES

The effect of contributions to the water of organic matter from external sources is manifest in all lakes that have affluents and in many others. Increase of color in the water is an obvious symptom of their presence (Table I), and decrease in the percentile value of protein and plankton furnish quantitative evidence of their amount. External sources contribute little or nothing to lakes whose carbon is only 1-2 mg/1. Table II shows that plankton is one-fifth of dissolved organic when C = 1.0-1.9 mg/1; this ratio, as shown in the table, steadily decreases as carbon rises, until when C = 20 mg/1 or more it is less than one-twentieth. The color of the water is near zero when carbon is at a minimum and it is more than 100 when carbon is at a maximum. (Table I.)

A direct quantitative relation may be traced between plankton and organic solutes in those lakes whose water receives a minimum amount of extractives from external sources. There are 60 lakes whose mean amount of organic carbon is less than 3 mg/1; their color is recorded as zero or very low. In these lakes the plankton has a mean value of 0.758 mg/1 and the dissolved organic is 4.15 mg/1, or slightly less than 5.5 times as much. There are 57 lakes whose color is recorded as zero; these include 26 lakes of the groups named above and 31 others; the mean value of the organic carbon is 3.1 mg/1. These lakes have plankton whose mean amount is 0.825 mg/1; that of the dissolved organic is 5.48 mg/1, a little more than 6.5 times as much. In the 13 cases discussed on p. 467 the plankton determinations are independent of those used in the two series above and the quantity of dissolved organic is 6 times that of the plankton. It thus appears that in lakes of this type the amount of dissolved organic content of the water is from 5.5 to 6.5 times that of the plankton, and that 6 times the plankton would be a fair average result. The absence of color in these lakes shows that they derive very little organic matter from their environment; probably a small but unknown amount comes by solution from the organic content of the mud. But this must be small, both because the color of the water is low and because these lakes are deep enough to have a thermocline, which shuts off the mud, or most of it, from direct connection with the epilimnion in summer.

We may, therefore, conclude that the plankton is the primary source of about 6 times its own weight of dissolved organic matter in the waters of those lakes which derive little or no organic matter from outside sources. In such lakes the mean relation between particulate and dissolved organic matter is fairly constant; at least, during that season of the year in which our studies have been made. A large temporary crop of algae raises the percentage of plankton in the total; just after the disappearance of such a crop the percentage is abnormally small, since dissolved matter still contains a

large amount of extractives from the vanished crop. But the average results are not widely variable.

Figures 2 and 4 and Table II show that in these lakes crude protein of the dissolved organic has a mean value of about 24 per cent; about two-thirds of that found in the plankton and less than one-half of the percentage found in plankton organisms (Fig. 3). Thus the organic matter of plankton organisms in passing through the stages of particulate and centrifugible plankton to those of solutes loses much of its nitrogenous content, leaving the percentage of carbohydrate at a far higher level than it holds in the organisms. This percentage is about 72 as compared with mean values of 35 to 47 per cent for plankton organisms and 59 per cent in the plankton itself. Ether extract under these conditions makes up about 2 per cent of the total.

Such is the situation in lakes with the clearest water, those whose organic matter is mainly derived from internal sources. Their number in the District, as employed in this discussion, is 88, out of a total of 529 lakes. No lake with so much as 5 mg/l of carbon gets into this group and very few of those with 4 mg/l. In the water of all of the other lakes there is present organic matter plainly derived from external sources, chiefly extractives from marsh or peat.

Attempts at a quantitative distribution of solutes to their sources

Organic matter from external sources assumes an increasing importance in lakes with larger amounts of total organic, as is shown by Table II and by the diagrams of Figures 2 and 3. The question therefore arises whether it is not possible in all of these cases to distribute this total organic to its two sources, external and internal. At first it seems that this can easily be done. We may make a rough estimate of that part of total organic derived from plankton by assuming that in all cases the plankton is able to maintain about six times its weight of dissolved organic matter, as seems to be the case in the lakes with clearest water. The results are not unreasonable when thus applied to total organic content of dissolved matter. For instance, in lakes with carbon of 20 mg/l or more the plankton is 2.22 mg/l, and the dissolved organic is 48.14 mg/l. We may conclude that plankton should supply about 12 mg/l of this or about one-fourth of the total. By a similar computation, plankton should furnish nearly one-third of the dissolved organic matter in lakes whose carbon is 15 mg/l; it should supply more than one-half where carbon is 10 mg/l; and about three-fourths where carbon is 5 mg/l. These estimates do not look unreasonable and no doubt there is a measure of truth in them, perhaps a large measure if we are content to leave matters at this point. But if we attempt to carry them out further we en-

counter difficulties and find that the situation is not so simple. For example, we may estimate that the dissolved matter derived from plankton contains 20 per cent of crude protein, a mean percentage smaller than that found in the lakes with clearest waters. We may apply this percentage in the case of waters whose carbon is 20 mg/l and for which we estimate 12 mg/l of organic matter derived from plankton. Then we discover that there is left for the organic matter derived from exterior sources, only about 6 per cent of protein, less than half of the mean amount found in marsh waters as shown in Figure 4, smaller than that found in 39 out of 41 marsh waters. On the other hand, the application of the mean percentage of crude protein found in marsh waters to the marsh extractives of the same group of lakes would leave practically no protein for the dissolved matter derived from plankton. The same general results follow the attempt thus to apply our computations to other groups, the discrepancies decreasing as we pass to groups of lakes in which the amount of organic carbon is smaller.

A situation not dissimilar arises if we attempt to distribute the crude protein of centrifuge plankton to the two types of substances contained in it, the living organisms and the partially decomposed organic particles derived from them and from other sources. It appears that in Trout Lake the centrifugible entomostraca and rotifers may constitute as much as 28 per cent of the total organic plankton. If this estimate is even approximately correct, we can hardly assign less than half of the plankton to algae and animals. Their crude protein would be more than 50 per cent of their organic matter and there would be left less than half that percentage for the remainder of the plankton. This is about the percentage found in the organic solutes from the clearest waters.

These attempts at a quantitative assignment of organic matter to its sources have been given partly to illustrate the complexity of the processes going on in a lake, and partly to show how great is our ignorance of the processes on which depend the production and the maintenance of its fundamental food-stuffs. They may also serve to show a possible resemblance of processes within the lake to processes that are active outside of it, and to indicate lines of investigation which may bring enlightenment.

It appears that proteins in the water disappear by decomposition more rapidly than do carbohydrates, thus bringing about a fall in the percentages of protein as we pass from organisms to organic solutes. It seems also that part of the proteins of organisms disappears very rapidly when these organisms die, but that after a certain part has thus disappeared the remainder is much more stable. This result is indicated by many facts, among them the resemblance of organic solutes from the surface water of lakes and from depths too great for direct addition from growing plankton.

It appears also that the proteins of the organic matter extracted from

marsh and peat are of these two types; that part of such proteins disappears soon after its entry into the lake, while part remains as a much more permanent addition to the organic content of the water.

Statements similar to these hold true of the processes by which vegetation is converted into peat, and which have been the subject of much study, especially by Waksman and his associates. In this study the tentative conclusion has been reached that the residual and more permanent proteins have entered into a resistant compound with non-nitrogenous substances. Investigation may show that in lake waters also the processes are similar and are leading to similar results.*

ETHER EXTRACT OR FAT IN DISSOLVED ORGANIC

We have said that few definite statements can be made regarding the quantitative relations of the ether extract in the course of the changes which the organic content of plants and animals undergoes in passing into solutes. The percentage of fat decreases, partly by losses due to decomposition and settling; and partly by the addition of solutes low in fat.

One or two definite results, however, appear from the large number of analyses that we have made. First, we have not found that the dissolved organic of any lake is without fat. A negative result was reported for a very few analyses, but in every case a redetermination showed the presence of an appreciable amount of fat. Second, the mean result is to show that the fat content of the residues is about twice that of the plankton found with them.

The amount of fat in dissolved organic matter is so small that the statement of Krogh and Lange (1931) holds true for practical purposes: "Sie können als Protein und Kolehydrat (ohne Fette) berechnet werden." But this method, if applied to our lakes, will always leave a small error and one which in some cases will be quite appreciable.

OTHER SOURCES OF ORGANIC MATTER

There are certain actual and possible sources of organic matter in lakes which have not been mentioned in these discussions. The most important of these, by far, is the ground water, which has an especial significance for seepage lakes. It has been omitted because of our ignorance of the facts; for no careful study of the subject has been made. We have numerous determinations of organic matter from well waters; but these do not yield results of quantitative value in this discussion. They show that wells often serve as accumulators of organic matter; and it is very doubtful whether they fairly represent the ground water.

Ground water itself offers numerous questions whose answers will be hard to find. It will be hard to determine so fundamental a matter as the quantity of ground water received by a lake, as compared with that coming

* See the papers of Waksman and his colleagues; and on the last point, see Waksman and Storey, 1932.

directly from rain. So too, nothing is known of the relation of ground water to run-off from melting snow or frozen ground. We therefore leave the whole matter to the future; with the general statement that ground water, as such and as distinguished from seepage water of marshes, etc., can contribute only a small part of the total organic; but a part which is doubtless significant in lake waters whose organic content is small. All preceding statements regarding such lake waters should be read with this possibility in mind.

SUMMARY

1. The organic content of lake water is mechanically separated into two parts by the centrifuge, which extracts the particulate material, constituting *plankton*. The part left behind is called *dissolved*.

2. Total organic matter has two sources, external and internal to the lake. Internal sources are plankton (the main source), mud on the bottom, higher plants, etc. External sources are humus, marsh, and peat; extractives from which are brought into the lake with entering water.

3. In lake waters with a minimum of external organic, the total organic is 3-6 mg/l; plankton constitutes 15%-18% of this.

4. In these cases dissolved organic contains, as a mean amount, crude protein, 24%; ether extract, 2.5%; carbohydrate, 73.5%; plankton, 16% of total. In extreme cases protein may be 40%; ether extract, 5%.

5. In most of these lakes extractives from marsh, etc., furnish an appreciable part of total organic and in many lakes a large part. Their presence is indicated by color of water and by lowered percentage of protein.

6. The "average lake" of the District contains 16-17 mg/l of total organic; plankton is 8-9% of this. Crude protein is about 15% of dissolved organic; ether extract less than 1%; carbohydrate, about 83%.

7. With extreme amount of extractives, total organic may exceed 50 mg/l; with protein, 8%; ether extract, 0.4%; carbohydrate, 91.5%; plankton, 3-4% of total.

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ECOLOGY OF LAKE FISHES

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In general organisms live in situations where they are able without particular danger to secure energy and at the same time avoid competition with other species. Animals depend more on food than radiation for energy. Of course each species is more or less limited to a particular habitat by its system of activities and by its behavior pattern. Where most energy is to be found conditions of life are severe because many of the natural phenomena which constitute environment are most variable. The active, speedy, and progressive land animals live where life is hard. As they need much energy many of them are active only during the warmest and lightest seasons or parts of the day. The animals which have retired to the seclusion of caves or the depths of lakes have attained the stability that obtains with an unvarying environment, but they must continually look toward the outside world for energy. They are safe and stable, but necessarily slow—slow-living, slow-moving, slow-thinking. They have difficulty in getting energy to keep their living machines going.

In lakes, as elsewhere, animals are sorted into strata, or zones, more or less according to available energy. In studying the cenotes in Yucatan the writer was greatly interested in the food of the fishes which commonly dwell in these deep, well-like lakes. The water in the cenotes usually contains little plankton and the bottom is covered with clean stones or is made inaccessible by stagnation and the presence of hydrogen sulphide. The cenote catfishes subsist on insects, spiders, leaves, fruits, blossoms, feathers—almost anything organic that falls into the water. Only in the darkest caves are they forced to eat bottom mud. Even in great, fertile lakes the food of animals which live in deep water must come directly or indirectly from the surface. Once the writer examined a lake trout which had just been caught in Lake Michigan at a depth of seventy fathoms, twelve miles from shore. Its stomach contained three grasshoppers and in the intestine were the remains of others.

Dr. Krogh has expressed the view that such animals as worms, molluscs, vertebrates, and arthropods do not feed on dissolved or colloidal organic matter. The distribution and observed foods of fishes in lakes appear to support this view, but there may be some question in regard to arthropods. Hinman (1930, 1932) has recently demonstrated that mosquito larvae can grow from egg to maturity in sterile water without solid food if they are supplied with organic solutes and colloids. Apparently no food is taken through the integument but water equal to 20 to 200 times the volume of a

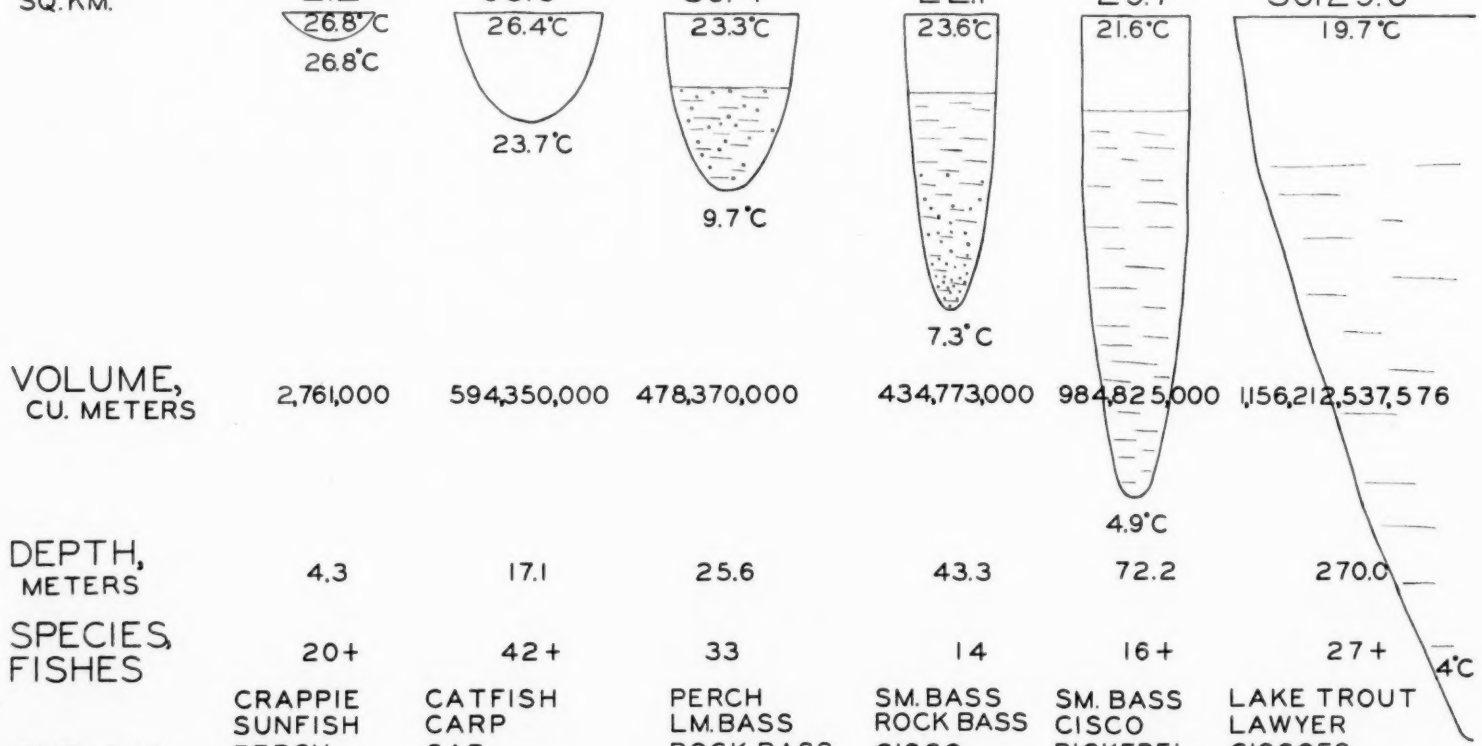
larva may pass through the enteron daily. Thus there is opportunity for the absorption of nutrients through the wall of the gut. These observations on mosquitoes raise the question as to whether the rather closely related dipterous larvae which occur in great numbers at the bottoms of lakes may not be able to feed in a similar manner. There are many mysteries still submerged in the depths of lakes. These must await some investigator who will bring them to light.

The lakes in northern North America show marked individual differences in the character of their fishes. Each lake is productive or unproductive, produces desirable or undesirable fishes according to the particular complex of environmental factors that it possesses. The fishes in six different types of lakes in Wisconsin have been studied at all seasons in an attempt to determine the relation of species to environmental factors (Pearse, 1921). The number and species of fishes present in lakes were determined by setting a line of gill nets which was four feet high and had a total length of 375 feet. It was divided into five 75-foot sections which contained nets of the following meshes: ¾, 1, 1½, 2, and 3 inches. When such a line of nets was set for 24-hour periods at various depths and in various situations a lake could be calibrated in terms of "catch-per-hour." A comparison of the mature fishes in different types of lakes was thus made possible.

The foods and parasites of the fishes caught were studied, the former being estimated in terms of percentage by volume. Young fishes commonly eat little else but small organisms such as algae, protozoans, rotifers, and microscopic crustaceans but adult fishes in the five true lakes[1] under consideration subsisted on the following foods in the percentages indicated: birds, 0.03; fishes, 17.35; immature insects, 23.66; adult insects, 6.12; mites, 0.25; crayfishes, 6.62; Mysis, 2.26; amphipods, 5.84; isopods, 0.19; cladocerans, 13.64; copepods, 1.70; ostracods, 2.58; clams, 1.69; snails, 3.46; leeches, 0.22; oligochaetes, 2.16; nematodes, +; rotifers, 0.24; sponges, 0.01; protozoans, 0.02; vascular plants, 3.23; algae, 1.86; and mud, 5.10.

Adult lakes fishes are chiefly found alongshore, especially where there is aquatic vegetation, and near the bottom in deep water. Few range into the open water in the middle of lakes, except the ciscoes and the species which prey upon them. The plankton eaters in the lakes under consideration are to be classified largely among river and pond fishes, though again the ciscoes in deep lakes are an exception. On the whole fishes seem to remain close to their food supplies in the littoral and profundal regions. However, in Lake Pepin, which is an expansion of the Mississippi River, and to some extent in other lakes various species of fishes leave the frozen littoral region in winter and remain for several months in deep water. Certain species of lake fishes do not feed at low temperatures. Others take less food and all

[1] The foods of the fishes from Lake Wingra, which is properly classified as a pond, are not included.



LAKE	WINGRA	PEPIN	MENDOTA	GENEVA	GREEN	MICHIGAN
AREA, SQ. KM.	2.2	65.0	39.4	22.1	29.7	36129.6
VOLUME, CU. METERS	2,761,000	594,350,000	478,370,000	434,773,000	984,825,000	1,156,212,537,576
DEPTH, METERS	4.3	17.1	25.6	43.3	72.2	270.0
SPECIES, FISHES	20+	42+	33	14	16+	27+
TYPICAL FISHES	CRAPPIE SUNFISH PERCH CARP DOGFISH	CATFISH CARP GAR SPOONBILL STURGEON SUCKERS WALLEYED PIKE	PERCH LM. BASS ROCK BASS WHITE BASS (CISCO) (DOGFISH)	SM. BASS ROCK BASS CISCO W.E. PIKE PERCH PICKEREL (TROUT)	SM. BASS CISCO PICKEREL ROCK BASS W.E. PIKE	LAKE TROUT LAWYER CISCOES COTTIDS
CATCH, PER HOUR	7.703	2.553	5.050	3.285	3.677	3.280

FIG. 1. Conditions and fishes in six Wisconsin lakes in midsummer.

fishes doubtless digest foods more slowly at low temperatures than at high (Pearse 1924; Pearse and Achtenberg 1920). In Lake Mendota the hypolimnion is without oxygen for about three months in summer. Most fishes are then prevented from visiting the rich food supplies on the bottom.

Figure 1 summarizes certain of the facts about the six lakes studied in Wisconsin. Lake Wingra is really a shallow pond which does not stratify or stagnate in summer. Lake Pepin is an expansion of the Mississippi River which shows little stratification and is usually turbid. Lake Mendota and Lake Geneva are eutrophic. The former is without oxygen in the hypolimnion in summer and for a short period in deep water in winter; the latter loses its oxygen only in the deeper parts of its hypolimnion in summer. Green Lake and Lake Michigan are oligotrophic. Their deeper parts have ample oxygen for respiration at all seasons and remain at low temperatures even in midsummer.

The productivity of a lake is indicated by the number and quality of its plants and animals. Judged by catch per hour in gill nets there are most fishes per unit of area in "Lake" Wingra. This pond has such fishes as the crappie, sunfish, carp, and dogfish among its dominant species. These are unimportant or absent from the true lakes studied. Lake Pepin shows the greatest variety of species but the smallest number of individuals per unit area. Its food resources which are available to fishes are not great. Many types of fishes use this lake as a highway and find food in its tributary waters. Lake Mendota, though stagnant in its deeper water for a considerable part of each year, contains a large number of species and individuals which are quite desirable and of fair size. The yellow perch, *Perca flavescens* (Mitchill), is present in enormous numbers (?15,000,000; Pearse and Achtenberg 1920). Though it attains larger average size in certain lakes of other types, it is to be looked upon as the dominant fish in this lake. It is particularly suited to rich, muddy, eutrophic lakes (Pearse and Achtenberg 1920). It eats a variety of foods and occupies a variety of habitats, though most individuals remain in as deep water as possible at all seasons. It is able to live for two hours in water which contains no oxygen and therefore can go into the hypolimnion to obtain food in summer. Few ciscoes are present in Lake Mendota, probably because lack of oxygen in the deep, cool water in summer is unfavorable. In deeper, cooler, clearer, pebbly-shored Lake Geneva ciscoes are abundant and perch are fewer than in Lake Mendota. Game fishes such as the smallmouth black bass, *Micropterus dolomieu* Lacépède, and walleyed pike, *Stizostedion vitreum* (Mitchill), are characteristic. In Green Lake there is a barren zone in summer between depths of 15 and 40 meters where no fishes are caught in gill nets. A group of littoral fishes lives near the surface; ciscoes swim in the cool water near the bottom, where they feed on amphipods (61.2%), clams (9.9%), ooze (8.2%),

Mysis (4.7%), and other things. In Lake Michigan a condition similar to that in Green Lake obtains but is more extreme. There is a fringe of littoral fishes but the great bulk of the fish population consists of deep water types.

In all five of the Wisconsin lakes investigated more fishes were found per unit area in the littoral than in deeper waters. In more or less clear lakes (Geneva, Green, Michigan, Mendota) most fishes were caught in the second five meters below the surface, but in turbid Lake Pepin in summer more were caught in the first and third than in the second. Large aquatic plants grew at greater depths in clear lakes and there were few or none along the shores of Lake Pepin. Light, wave motion, shelter, and other factors contribute to bring about the arrangement of plants and animals in more or less definite strata.

In a general way the productivity of a lake in fishes is related to the biomass but the quality of the fishes in a lake depends upon a variety of environmental factors. Usually most fishes per unit area occur in muddy, vegetation-filled, shallow ponds (Lake Wingra), but the characteristic fishes (carp, crappie, sunfish, dogfish) are not the most desirable for food. Rich eutrophic lakes (Mendota) produce considerable quantities of desirable fishes (perch, largemouth bass, white bass, rock bass). Oligotrophic lakes (Green) produce littoral game fishes of good quality and size (smallmouth bass, wall-eyed pike, pickerel) and ciscoes in deep water. Lake Geneva, intermediate between eutrophic and oligotrophic types, is perhaps the best from a sports-man's point of view. It produces many game fishes of considerable size (smallmouth bass, pickerel, rock bass, even trout at times) and ciscoes. Commercial fisheries to be successful in inland waters must have a continual supply of rather large fishes. Such a supply is to be found only in large lakes. A lake of limited volume (Lake Mendota) cannot furnish fishes of large size, such as the carp and buffalo, for a long period and commercial fishing is profitable for only a week or two annually. Lake Michigan, with its scantier population but enormous area, and Lake Pepin, with food re-sources in tributary rivers and swampy areas, repay exploitation throughout the year.

Each lake presents a type in which one or more species of fishes may be at their best and become dominant. The yellow perch occurs in all six of the lakes studied. In Lake Wingra perch are numerous but small. In Lake Mendota they are abundant, dominant and of good size. In Lake Pepin, Green Lake, Lake Geneva, and Lake Michigan they are not numerous but are at times of good size. Along the muddy shores of Lake Mendota fish-eating largemouth black bass are common and the more insectivorous small-mouth black bass are rare; but along the pebbly and sandy shores of Lake Geneva and Green Lake the opposite is true.

Lake fishes which live in deep water usually do not migrate rapidly from

one level to another. However, they commonly visit shallow water to breed once each year. Thus the adult deep-water fishes live where temperatures are low, but their young have opportunity for a time to grow more rapidly at higher temperatures and may have the advantages of freshly energized littoral foods and littoral shelters. Such fishes during most of their lives depend for energy largely on the food that settles to or develops in or near the bottom mud. To a less extent they consume plankton organisms, which in turn derive their energy from above. At times there is lack of oxygen in profundal regions. This makes it impossible for certain types of fishes to exist there. How the many animals which live and remain active in bottom muds for long periods without oxygen carry on metabolism is still somewhat of a mystery. Cole (1921) believes that decomposing plant remains may liberate an oxidizing substance which can supply oxygen to bottom animals. Perhaps certain profundal bottom animals are not only able to live without oxygen but are also capable of subsisting on dissolved or colloidal organic food (Hinman 1930). Fishes apparently do not do so.

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THE BIOCHEMISTRY OF THE INVERTEBRATES OF THE SEA

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The rise of experimental biology during the last three decades has distracted the attention of zoölogists from purely morphological and taxonomic problems which were predominant during the last century and has resulted in numerous attempts at unravelling the intricate relations that unite the organism with its environment. Since the time of Cuvier, whose point of view was formulated with great clearness in the report concerning the state of sciences submitted to the Emperor Napoleon (Cuvier, 1827), throughout the 19th century the form of the organism was regarded as more essential than the material from which living things are made. Modern research pays more attention, however, to the latter and attempts to determine to what extent the organisms can be affected by the outside forces, and which of their morphological and functional characteristics being determined by heredity remain stable. The analysis of the relations between living matter and the surrounding medium leads to the conclusion that the conception of an organism, as a unity independent of its environment, exists only as an abstract mental picture. This idea is best formulated by Houssay (1910, 1920) who calls our attention to the lack of correspondence between the organism pictured in the mind of the biologist and the actual living thing. His point of view that the organism and its environment form two phases of a mutually continuous system differs from the generally accepted one which considers the organism as being definitely separated from its environment by the limiting surfaces of its body and studies the former independently from the medium in which it lives. Although from a theoretical point of view Houssay's idea is applicable to all organisms, aquatic as well as terrestrial, its application to the problems of oceanic and freshwater biology is especially profitable because in an aqueous medium the living matter is more intimately related to its environment than that of land and air. There are many aquatic forms, for instance sponges, coelenterates, and others the bodies of which are not as definitely shaped as are the bodies of terrestrial organisms. Moreover, in many of them sea water penetrates the tissues and takes the place of the blood of higher forms. It is remarkable, for instance, that there exists a great similarity between the mineral content of the blood of vertebrates and higher crustacea and that of the sea water, although the concentration of ions entering into the composition of both media is different. This fact lead to many interesting speculations which, however, are beyond the scope of the present review. (McCollum, 1926.)

We can think of the organisms of the sea as being in a dynamic equilibrium with the medium in which they live. They are constantly affected by the latter and in turn exert on it a profound influence by altering its chemical composition and physical properties. Living forms possess a remarkable ability of extracting various elements from the solution and in concentrating them in their bodies. After death the accumulated material is redissolved or, being deposited on the bottom, undergoes further changes, participating in the formation of various minerals of sedimentary rocks. Thus, the living matter forms an important link in the chain of cyclic processes that go on without interruption in the ocean. At present the rôle of organisms in the cycles of various elements has been demonstrated for Al, As, B, Ba, C, Ca, Cl, Cu, Fe, F, H, K, Mg, Mn, N, Na, Ni, O, P, Pl, S, Si, Sn, St, Ti, V, and Zn. As to their rôle in the formation of various minerals the reader is referred to the mineralogical papers of Samoilov (1917) and Vernadsky (1923, 1924).

The chemical activity of living organisms as accumulators of various elements can be understood by comparing their chemical composition with that of sea water. Such comparison shows that although the bodies of various forms are comprised of the same elements which enter into the composition of the sea water, the quantitative relations of the components are different. Vernadsky (1923) and Vinogradov (1931) have shown that the following elements are concentrated in various marine forms: Ca, Cu, F, B, K, As, Si, P, I, Fe, and Zn.

It is interesting to note that Na, Cl, and Mg, the physiological rôles of which are well known, are not accumulated by living matter. One must bear in mind that our present knowledge of the chemical properties of sea water is very inadequate and the presence of several elements, for example vanadium, which has been found only in organisms, must be assumed.

On the basis of elementary chemical composition all marine organisms can be grouped according to the elements they concentrate in their bodies. Thus we can speak of the concentrators of calcium (foraminifera, coelenterata, bryozoa, endinodermeta, mollusca, vertebrata) silicon (diatoms, sponges, radiolaria) iron (bacteria, foraminifera, mollusca), copper (decapoda, mollusca) vanadium (Ascidia, Stichopus) zinc (lamellibranchia, coelenterata) iodine (gorgonia, sponges, mollusca) strontium (radiolaria) and so on. In many instances the physiological significance of the accumulated material is obvious. Thus salts of calcium, magnesium and silicon are used for building skeletons and shells; iron and copper enter into the composition of blood pigments, haemoglobin and haemocyanin. Vanadium, so far found only in Ascidia and Stichopus, apparently plays a similar rôle in the blood of these animals. In connection with its occurrence (Henze, M., 1913, Phillips, 1918) it is interesting to note that this strong catalyst was found only in the

blood of sedentary and sluggish organisms as Ascidia and Stichopus, the rate of metabolism of which is probably very slow.

ACCUMULATION OF ZINC

Zinc is accumulated by the tissues of jelly fishes, shrimps, crabs, but is especially abundant in the gastropods—Sycotypus canaliculatus, Fulger carica, Urosalpinx cinerea, and in lamellibranchs—Ostrea, Venus, and Pecten (Mendel and Bradley, 1905; Vinogradov, 1928). In the oyster it occurs in very large quantities varying from 26 to 2,298 mg. per kilo of fresh meat (Hiltner and Wichmann, 1919). Similar to the conditions found in Sycotypus, zinc in the oyster probably always is associated with copper, although there is no uniformity of ratio of zinc to copper nor has any correlation been found between the zinc content of the oyster and the water in which it grew. Oysters living in waters not contaminated by industrial wastes may contain in their tissues more than 35,000 times as much zinc as is present in an equivalent weight of water (Bodansky, 1920). Zinc is distributed rather uniformly throughout the body with the exception of muscle which contains less of it than do the other tissues. In other forms like jelly fishes, shrimps, and crabs, the zinc content is much less than in the oyster, varying between 4.50 to 22.80 mg. per kilo of fresh meat. Its amount in clams approaches that in the oysters, i.e., 77 mg. per kilo, fresh basis.

The biological rôle of this metal is but little understood. In *Sycotypus canaliculatus* it forms an essential constituent of the respiratory pigment, hemosycotypin, which is probably analogous to haemocyanin (Mendel and Bradley, 1906-7).* Its rôle in oysters and clams and other organisms remains to be determined. It is interesting to note that in herring zinc is accumulated in the testes during the period of maturity (Bertrand and Vladesco, quoted from Vinogradov, 1928), and that a minute quantity of this metal (1:500,000) has a stimulatory effect on growth of moulds, *Aspergillus niger, Sterogmatocystes nigra* (Raulin, 1870, Bertrand and Javillier, 1912). Obviously no generalization from these fragmentary observations is possible until a more thorough study is made.

ACCUMULATION OF IODINE

Iodine presents another example of an element which occurs in the sea water in a highly dispersed state (0.00035 mg. per kilo, Thompson and Robinson, 1932) and is accumulated by algae, gorgonacea, sponges, molluscs, crustacea, and fishes. The highest content was found in *Gorgonia clavellina* in which iodine reaches 7.8 per cent of dry substance. The iodine content of oysters from all parts of the United States coast was recently studied by Coulson, Remington, and Levine (1933, in press). The result of their inves-

* According to M. Florkin whose book "Transporteurs d'oxygène," 1934, Paris, came to my attention after this paper was written, hemosycotypin contains no molecule of zinc and the term should be abandoned.

tigation presented in Table I is of great interest because it shows that the iodine content of *Ostrea virginica* is not a specific character remaining constant in all the samples regardless of their origin, but varies both with the locality and season. As one can notice from an examination of this table there is a marked difference between the spring and winter samples taken in California and in the Gulf of Mexico. The significance of these changes remains to be ascertained by further investigations.

TABLE I. Average iodine content of American oysters (mg. per kilo dry basis).

LOCALITY	*Spring*	*Winter*
N. Atlantic	2.028	2.977
S. Atlantic	3.304	3.423
Gulf of Mexico	3.461	3.254
Pacific	2.050	1.834

The variation on the iodine content of individual samples is much greater ranging from 1.090 to 15.800 mg. per kilo of dry substance.

Experiments carried on since 1929 at Arcachon, France, on the European oysters, *Gryphea angulata* and *Ostrea edulis* throw some light on the behavior of iodine in the sea and in animal tissues. According to Loubatié (1931) free iodine, added to the sea water immediately combines with the protoplasm of algae and minute phytoplanktonic organisms. Thus, Fucus normally containing on the average 0.08 mg. I per kilo (fresh basis) after being kept for six days in the iodized water accumulated 435 mg. per kilo. Portuguese oysters, *Gryphaea angulata* placed in unfiltered sea water containing 150 mg. iodine per each liter accumulated 700 times more iodine than they normally contain. The superiodized oysters continue to feed normally and their other functions apparently are not disturbed. By the end of the fourth day of exposure in iodized water the accumulation of iodine reaches its maximum, namely 1 mg. per 10 grams of live tissue and thereafter remains constant. Judging by the intensity of the reaction the iodine is located chiefly in the cells of the gills, then in the muscle and mantle. The reaction is always negative in the region of gonads (Turchini, 1930).

From the observations on iodine content of oysters from different localities and from the results of the experiments of French investigators the inference can be drawn that this element can be stored in the tissues far in excess of its normal requirements by the organism. Although the significance of iodine in the nutrition of mammals is well understood its physiological rôle in the metabolism of marine invertebrates is entirely unknown.

ACCUMULATION OF IRON AND COPPER

Accumulation of iron and copper presents another example of the correlation between the metal content of the organisms and the environment. Both metals are important constituents of the blood pigments and are therefore primarily concerned with the respiratory functions of the organisms. However, in oysters both metals may be stored far in excess of their normal

requirements. It has been known for a long time that in certain localities oysters accumulate so large an amount of copper as to render them greenish and unpalatable. Along the coast of British Isles the variation in the proportion of copper in the fresh oyster meats shows a range between 40 and 1,000 mg. per kilo. One exceptional specimen was found to contain 24 milligrams of copper, a proportion of 3,300 mg. to one kilo (Orton, 1923).

The highest copper content in the American oyster, 1,487 mg. per kilo of fresh meat was found in the samples taken at Perth Amboy, N. J., where the oyster beds are located not far from large copper refineries and other metallurgical works (Hiltner and Wichmann, 1919). There is no doubt that the intensity of green coloration of the American oyster is associated with increase in the copper content. The green pigment passes through a collodion membrane which holds back congo red, is not precipitated by sodium sulphate and therefore is not haemocyanin or copper proteinate of any kind (Galtsoff and Whipple, 1931). Although its chemical nature remains to be determined it has been found that it exists in a highly dissociated state and is of a small molecular size.

Iron is always present in oyster tissues although its presence is not manifested by abnormal coloration. Author's observations of 1932-1933 on oysters grown in Long Island Sound (unpublished data) show that within a limited area of Milford Bay the iron content of oysters is variable, ranging between 19.07 and 57.07 mg. per kilo of fresh substance. Copper content of the same oysters is, however, much higher, ranging between 72 and 431.9 mg. per kilo. It is expected that the investigation which is now being carried on will throw light on the question of seasonal changes in the metal content of the oysters and will determine whether there is a correlation between the accumulation of iron and copper.

That there exists definite correlation between the Fe and Cu content of oysters and their geographical distribution has been shown by the work of Coulson, Remington and Levine (1932). An examination of Figure 1 discloses that oysters from the North Atlantic States are poorer in iron and richer in copper while the reverse is true for the South Atlantic and Gulf oysters. The variation in the contents of these metals occurs gradually as we proceed along the coast from Rhode Island toward Florida. This suggests that the observed changes are not incidental but may be due to changes in the chemical composition of water. Unfortunately, no systematic analyses of the inshore waters are available. Indirect evidence corroborating our assumption can be obtained, however, from the data on the chemical composition of river waters discharged along the Atlantic slope. The results of the chemical analyses given by Clarke (1924) and presented in Table 2 show that the waters of the South Atlantic States (beginning with Dan River, Virginia) carry in solution a greater percentage of Fe_2O_3 than the rivers of

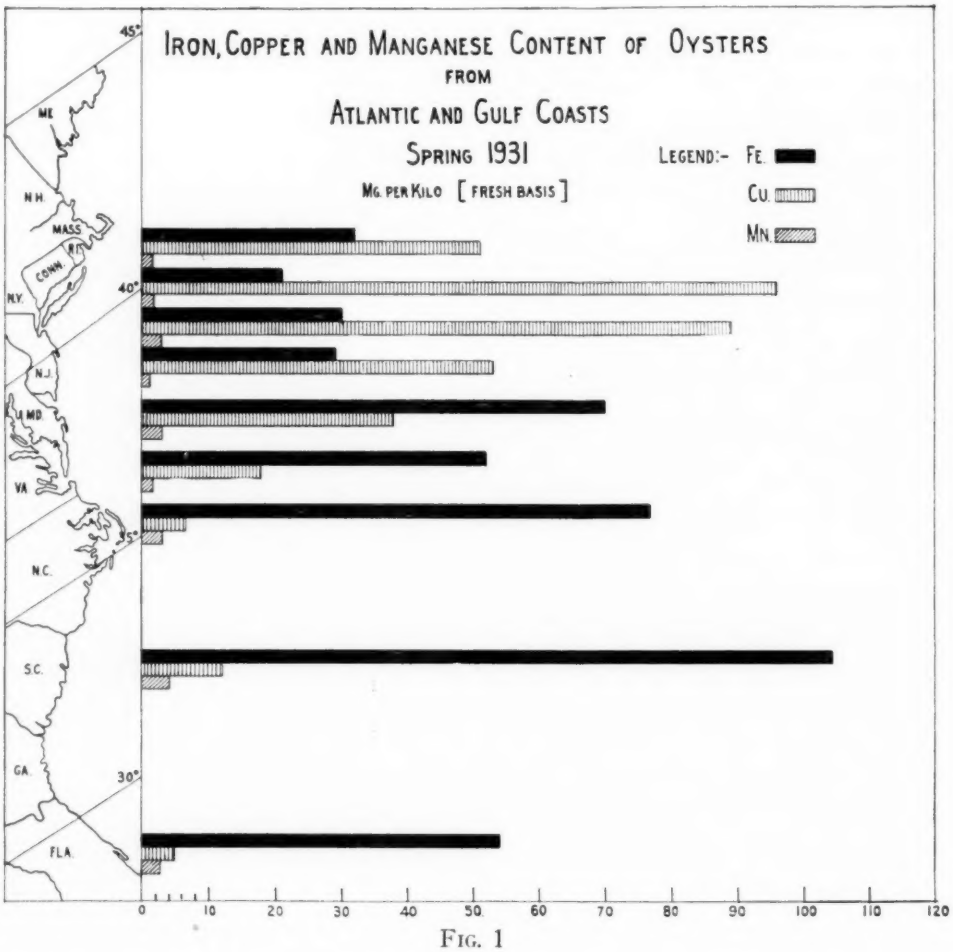

FIG. 1

Pennsylvania, New Jersey, and New York. The coincidence between the increase of iron in the southern rivers and its increase in the meats of oysters grown in South Atlantic States seems to be significant. Moreover, the majority of the rivers emptying into the Atlantic Ocean south of Chesapeake Bay carry in suspension a considerable load of red mud which undoubtedly contains a great deal of iron. According to the analysis given by Clarke (l.c. p. 445) the composite sample of terrigenous clays contains 5.07 per cent Fe_2O_3 and 2.30 per cent FeO.

TABLE 2. Iron content of river water (suspended sediments are not included).

Locality	*Per cent Fe_2O_3*	*Salinity, p. p. million*
Hudson River, near Hudson, N. Y.	0.20	108
Raritan River, N. J.	0.23	85
Delaware River at Lambertsville, N. J.	0.15	70
Susquehanna River at Danville, Pa.	0.11	112
Potomac River above Great Falls	0.09	101
James River at Richmond, Va.	0.85	89
Dan River at S. Boston, Va.	2.51	71

Roanoke River at Randolph, Va.	1.74	79
Neuse River at Raleigh, N. C.	2.88	79
Cape Fear at Wilmington, N. C.	2.16	73
Pedee River, N. C.	0.59	69
Saluda River near Columbia, S. C.	0.87	62
Wateree River near Camden, S. C.	0.60	73
Savannah River near Augusta, Ga.	0.91	60
Ocmulgee River near Macon, Ga.	1.83	69
Oconee River near Dulin, Ga.	1.43	68

The mechanism of accumulation of copper and iron by the oyster has not yet been determined, but from what we know regarding the feeding of the oyster it seems probable that the withdrawal of metallic salts is accomplished through the digestive tract. It is also possible that the oyster does not obtain all the metals directly from the solution or suspended inorganic particles but receives them with the microscopic algae which have already accumulated them in their protoplasm.

CHEMICAL COMPOSITIONS OF SKELETONS AND SHELLS

Material accumulated by the organisms is often used for the building up of skeleton, shells or other protective structures. On the basis of the chemical composition of the material used for this purpose we can distinguish the following main groups:

(1) Carbonate series comprises skeletons or shells made of aragonite, calcite ($CaCO_3$), dolomite ($CaCO\ MgCO_3$) and magnesite ($MgCO_3$). This type is represented by Foraminifera, Coelenterata, Echinodermata, Bryozoa (excepting Bugula which contain 2 per cent calcium phosphate), Polychaeta (excepting Eunicidae the tubes of which contain from 6.5 to 21.6 per cent P_2O_5), Mollusca and lower Crustacea.

(2) Phosphate series comprises skeletons made of calcium phosphate ($3Ca_3(PO_4)_2CaCO$) and apatite ($CaF.\ Ca_4P_3O_{12}$). This type and its modifications are found primarily in Vertebrates, Brachyopoda, and higher Crustacea (Stomatopoda and Decapoda). The latter besides apatite contain also carbonates of calcium and magnesium.

(3) Sulphate series comprises skeletons made of $BaSo_4$, $SrSO_4$, and $CaSO_4$. It has a limited distribution occurring in certain Rhizopoda ($BaSO_4$ in Xenophyophora) and Radiolaria ($SrSO_4$ in Podactinellus). On account of the solubility of calcium sulphate in water there are no shells which are made entirely of this salt, but the latter enters into composition of nearly all the structures.

(4) The Silicate series is primarily represented by Radiolaria and siliceous sponges.

All four series probably existed since the earliest geological eras although the siliceous organisms were predominant in the primeval ocean. Why in the course of animal evolution the siliceous skeleton failed to develop above

Radiolaria and sponges is, of course, a matter of speculation. There is no doubt that since the pre Cambrian times the composition and concentration of salts in the sea have undergone great changes which must have affected the evolutionary trend. There are reasons to maintain that the waters of the primeval ocean were rich in silica and deficient in calcium (Clarke, 1916; Samoilov, 1923). Whether these conditions determined the predominance of siliceous organisms can not be definitely proven, although the explanation is rather tempting. On the other hand, we have sufficient evidence to show that the presence of an element in a highly dispersed state in the sea does not preclude its withdrawal from the water and accumulation by the living matter. Only a complete absence of an element or its presence in a form unavailable to the organism may constitute a factor limiting the propagation of that particular species. Since we possess no information concerning the conditions of primeval ocean, rate of propagation of its inhabitants and their relative abundance, further speculation concerning the causes which influenced the development of the present day marine fauna seems to be futile.

Within one taxonomic group the chemical compositions of skeletons is to a certain extent dependent on the geographical distribution of the representatives of that group. Clarke and Kamm (1917) revealed an interesting fact that different species of starfishes show a progressive enrichment in magnesia from 7 to over 14 per cent following an increase in the temperature of their habitat. Similar observations were made on various species of Alcyonaria in which the per cent of $MgCo_3$ increases from 6.18, for the species living at 42°16′ N. lat. to 15.73 for those inhabiting tropical waters (3°50′ N. lat.).

We have no evidence, however, that the observed differences are due to the temperature. It is quite possible that the secretion of skeletons is influenced by other factors, as for instance chemical composition of water and food, which were not studied. It would be of interest to find out whether similar changes occur in one species which has a wide range of distribution.

The secretion of mineral skeletons and shells by marine organisms is a process of paramount importance in the cycles of various elements in the sea. Unfortunately, it has not yet been sufficiently studied.

It is a matter of common knowledge that shells of molluscs, otoliths, fish scales, and other structures have more or less distinct concentric rings indicating seasonal changes in the rate of deposition of the material from which they are built. Their presence permits the determination of the age of the individual with great accuracy. In connection with this it is interesting to mention that in the oyster the deposition of the shell material continues throughout the winter even when other activities of the organism are reduced to a minimum. By examining Figure 2 one can notice that the weight of the shell determined at biweekly intervals continued to increase when the tem-

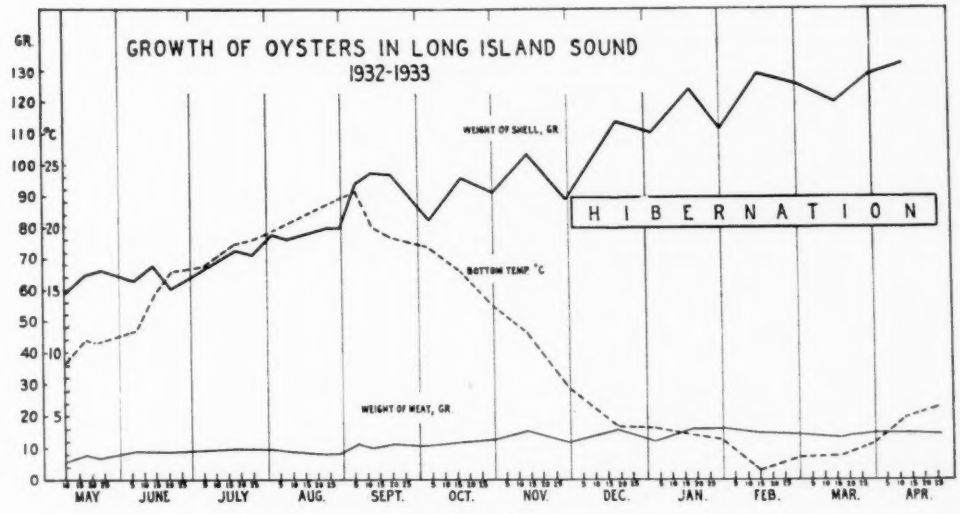

FIG. 2

perature of the water dropped below 4° C. and the oysters were in a state of hibernation. During all this period no trace of food was found in the digestive tract. The latter observation is in conformity with previous experimental work of the author (Galtsoff, 1928) on the effect of temperature on the activity of the ciliated epithelium. From the facts that shell continues to grow when no food is taken in, and the weight of the meat does not decrease, an inference can be made that calcium and other salts required for the building of shell are taken in directly from the sea water. Whether they are absorbed by the shell secreting tissues or through the digestive organs remains to be determined.

CONCLUSION

It was the purpose of this brief review to show that biochemical studies applied to oceanic biology open up a new and broad field of research. At present only scattered material is available which precludes any broad generalizations. Yet the problems outlined in this paper seem to be of great general interest. It is believed that their solution will throw more light on the factors that control the life in the sea.

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FAITH IN THE RESULTS OF CONTROLLED LABORATORY EXPERIMENTS AS APPLIED IN NATURE

By V. E. SHELFORD

[The introductory remarks of the discussion following the symposium on *Aquatic Animals and their Environment* at the summer meeting of the Ecological Society of America, in Chicago, 1933.]

With the initiation of experiments involving the control of external conditions in the field of biology, there was a strong tendency to imitate the methods of physics and chemistry. Constant temperatures were used, the ideal being to permit only fluctuations of less than a few hundredths of a degree. Unfortunately too many investigators being without means for the control of factors other than temperature, and without an adequate comprehension of the intricate network of related factors which make up the simplest environment, neglected other factors almost entirely and strove only to control temperature.

When one considers how rarely one finds a habitat in which conditions remain constant and at the same time a habitat which is available so that experimental materials may be collected from it, it is surprising that there have been so few attempts to bridge the gap between these physically ideal experiments and the variable nature of the environment in which most experimental animals naturally live.

The experimental ecologist, however, sometimes wishes that he could adhere to the methods of the mechanistic physiologist. There is a great satisfaction in very carefully setting up an experiment with its parallel check, in tying down all the easily recognized physical and chemical factors with mechanical controls so that only one factor is varied, and in taking careful readings over a period of 20 minutes, two hours, or longer as the case may be. The writer once believed that the problems of outdoor nature could be solved in that way. Experience has shown that they have to be approached from a different angle. There must be different background of theory and experience to motivate the experiments—a fact which those of us trained in experimental work were at first thought inclined not to believe.

The faith in these carefully controlled experiments taken alone has been and still is too great. The difficulties of working with nature, with all the multiple factors involved, are really very great, the solution of problems comes slowly, and they have to be approached from a viewpoint different from that of the mechanistic physiologist. It is true that conclusions drawn from the observation of organisms in their natural habitat are often shown to be incorrect or only partially correct when subjected to experimental tests. The reverse is also equally true. The conclusions drawn from careful laboratory experiments are found to be erroneous when put to a test in the

natural habitat. It is now nearly twenty years since Dr. Powers and the speaker did some work on salmon and herring. At that time it was supposed that when salmon found a stream it was through a recognition of salinity decrease at the mouth of a river. We found when we set up experiments that this was not true; it was hydrogen-ion concentration which fishes recognized. They selected a certain H-ion concentration. Later through field observations Dr. Powers thought herring were always associated with a certain hydrogen-ion concentration, but this did not prove true over a large geographical area. Later observation and some experiments showed that the salt content of the water modifies the hydrogen-ion concentration selected by the fish. Thus we build up multiple factor hypotheses for response rather than a single factor system.

The speaker had the experience of working for about ten or fifteen years on insects of economic importance. Many thousands of dollars were spent; few economic entomologists use these experimental results because they are too complicated. But our experience with them indicates that continuity of outdoor observation will often bring much more important results from a practical or theoretical standpoint than a long series of experiments conducted *without* such guides.

The organism used was the codling moth of the apple, and while extensive experiments were conducted with variable and constant temperatures and charts and tables indicating the rate of development at almost any temperature worked out, we did not get at any of the really important economic problems which concern this apple worm with as great success as we did with some very simple observations of a natural phenomenon made in another connection. We happened to observe the abundance of the codling moth larvae and their ability to over-winter in relation to rainfall.

During two or three years we got perhaps the great secret of the abundance of this insect in a particular year. If we had a heavy autumn rainfall, the larvae came through 95% alive in the spring, in great abundance, and if nothing else interfered, they went forward with a very large brood of moths. Perhaps that occupied a tenth of our time for two autumns and winters in connection with other work. This important fact was discovered in following a natural phenomenon and getting an organism's response to it. We secured perhaps more important results than with all the other work. So it was only recently when some entomologists came to the speaker and said they wanted to start some climate simulation experiments on a certain insect, this was his question: Do you have fifteen years of quantitative and naturalistic observations on this insect and its relation to weather conditions? And when they said no, our reply was: You had better make these observations first and set up experiments afterwards.

This symposium has been concerned with the organisms of the water in

relation to their environments, their metabolism, the solid food they secure and the dissolved substances they may use. Very little has been said about the physical environment. Physical environment often has profound effects on the abundance of food and various other physiological conditions which make for the growth of a great many organisms of a particular kind or of only a few, or of smaller or larger ones, and so forth.

Comparison of different habitats geographically separated often sheds important light on habitat relations. For example the five series of lakes which Drs. Birge and Juday are studying should afford many suggestions through comparisons of their gross living material, their dissolved and suspended organic matter, etc.

In addition to this geographic comparison, comparisons of conditions at different periods of time are of the utmost importance. The abundance of various organisms has been shown to fall in cycles. We have all heard of the 11-year sun spot period and the shorter periods which people have observed in connection with fishes and various northern animals. It appears that we should arrange to know the concentration of organic matter in water at a set of suitable stations over a rather long period of time, and its quantity compared with the abundance of certain organisms, perhaps the protozoa, which Dr. Krogh suggested are the small ones that can possibly absorb this organic matter. It would further appear that when organisms which might absorb such organic matter are very abundant, the organic matter might be expected to decrease, provided they use it extensively. If not, we would have indirect evidence to indicate whether or not it has accumulated over long periods. Again, when abundant organisms disintegrate and produce organic matter in quantity, the question is: Does that add to the total organic matter in the water at that time and in that region?

All these operations are important steps toward setting up critical experiments in aquaria and on organisms selected on the basis of their behavior in nature. These results must, however, be checked back against the natural habit and natural biotic community. This means a program which has continuity. Dr. Allen of the Scripps Institution has remarked that one of the most serious criticisms of nearly all the plankton work and other work of that sort on the sea is the fact that it lacks continuity; it has not been carried out long enough. Observations are too infrequent to enable one to know what really is the average occurrence of organisms in the sea. We hope that such continuous work may be carried on first in the form of direct observations, and then be used as a basis for experiments which may bridge the gap between the laboratory and the actual environment.

DISCUSSION

Dr. Birge: I have no question to bring up, but possibly I might speak a word in relation to the last remarks of yourself about continuous observa-

tions. The most interesting thing so far as I am concerned that we had presented here this afternoon was this relation between the plankton and the dissolved matter in those lakes in which the plankton is the source of this dissolved matter.

When we found that these lakes which number so many that we can't be seriously mistaken, five to six times as large a quantity of material in organic solution as organic particulate material, it seemed there was a hint for further observations. Of course, the trouble there is having money enough. We have been fortunate because we have been able to maintain a party for the past eight seasons in northern Wisconsin to carry on active explorations of this sort. Yet, if you are going to work out that relation between plankton and organic material, with the constant variation of the plankton going up and down all the time, with the constant variation of the dissolved material changing materially, and do that in a sufficient number of lakes so as to have something to tie to, you can figure up what it will cost and, if you are a good mathematician, where you will get the money. So we have to work bit by bit and trust that our grandchildren will be able to make a patchwork quilt out of pieces we have been able to bring together.

Take diagram Number 3 of mine, that was shown a while ago: This change of the constitution of the organic matter as you pass from the organism to plankton and from plankton to the dissolved material in the water, what are the substances that you find? How do these substances change? There you have a subject that involves an enormous amount of chemistry which has to be worked out by thoroughly good chemists and followed out not by just one line but by a lot of lines. And you are going to find it variable, shifting and the picture you would like to draw is not a picture of matter but a picture of probability. I suspect after a long time we shall still say we have drawn a picture of probability—and we do not even have that picture at present.

Dr. Shelford: Dr. Pearse has a statement about fish—where they get their food in the different kinds of lakes.

Dr. Pearse: In a lake like Michigan it practically all comes from the bottom, and the plankton is near the bottom.

Dr. Birge: Possibly it would be of interest to relate that the relation between plankton and centrifugable dissolved material is 6:1 in Lake Michigan, as indicated by the observations given. I suppose that this is on the order of 7 milligrams per liter; that is substantially what would correspond to 3½ milligrams of organic carbon per liter. That must be a product of the plankton, because the amount that comes in from rivers and Lake Michigan must be a very small amount in proportion to the cubic content of the lake.

Dr. Pearse: In Lake Michigan practically everything of food value is on or near the bottom but in Green Lake it is on the surface and below that there is a long gap down to 35 meters. In the summer you catch no fish at all in

this barren zone. Copepods are not a very large factor in the food of adult fishes. They are not much eaten; I do not know why.

Dr. Birge: Green Lake copepods have lots of fat in them.

Dr. Shelford: I wonder, Dr. Krogh, if it would not be easier to work out fluctuations of plankton and other organisms in the sea than in the lakes?

Dr. Krogh: I suppose it might be easier to do that, but it would need to be done far from shore, which introduces much expense.

Dr. Shelford: Of course all our difficulties are economic.

Dr. Krogh: I might just mention that I have been, of course, very greatly interested in the results with colloids. The colloids might be neutralized by animals. Still I hope it will be possible to determine the colloids in the sea water, and I hope to do it. I would like to go up to Woods Hole for some time. I might say in my figures on the colloids are probably excluded because of the precipitation.

Dr. Birge: In regard to the colloids and the amount of centrifugable material we get from the lakes, while we have no quantitative evidence in the matter, it seems as though we were centrifuging out from the water a certain amount of colloids. There is no reason, as I see it, why if the algae have colloid sheaths, why that colloid should not get loaded up with precipitated carbonates. Of course, this is all mere guess work. I see no reason why the colloids which come from the algae or the Crustacea with colloid shells, and Polypodium; why colloids should not get loaded up with precipitated carbonates, and centrifugable material. This would be available for the Daphnia to paw in with their legs and to feed upon. There is a problem which assuredly needs careful investigation and whose mysteries we have been unable to penetrate as yet. Have you put the colloids by themselves, and if so have you any solution for that problem?

Dr. Krogh: Not so far. I find it very difficult to assume that colloids could be filtered off. It would require very arduous work to get out the colloids. Still it may be possible that some colloids are precipitated down during the course of the process, I do not know. These colloids in fresh water consist to a large extent of inorganic materials—the inorganic materials consisting of at least three-fourths if not all of the total colloids.

Dr. Higgins: An interesting question has been turning over in my mind. In a self-contained system like the lake in which the total organic content of the water can be determined, the question of food changes doubtless is susceptible, we hope, of final solution. The question of food supply in the ocean, however, is somewhat different in that each section of the ocean is related to every other and because the size and section should be studied separately. I am thinking of conditions in the Bay of Fundy where investigations were carried on for two years by an International Commission studying the conditions which explain the remarkable concentration of the herring fisheries in

the vicinity of Passamaquoddy Bay which forms a part of the International boundary between Maine and New Brunswick. The young herring utilized as sardines are undoubtedly very much concentrated in this area. There has been the presumption and some evidence to support it that the unusual concentration of plankton in this area supported in turn by the remarkable mixing of viscid waters drawn in by the approximately 26 foot tides that occur in the Bay of Fundy explains this concentration. Examination of the phytoplankton and zooplankton show that the plankton is more abundant outside the area affected by the mixing. Plankton examinations conducted by Dr. Charles Fish indicate that the areas in which plankton is most abundant are those outside this same area where herring fisheries are located. The examination of the circulation itself by Dr. Watson of Queen's University shows that while there is a tremendous mixing in the passes leading to the Bay, the effect of this mixing may not extend very far from the passages. So the International Commission was faced with the necessity, at the end of the period of its investigation, when its funds were expended, of deciding that while conditions would be changed necessarily in Passamaquoddy Bay to such an extent that the herring fisheries would be virtually destroyed by the construction of the hydroelectric dam flowing into the Bay, it would not be affected outside the Bay.

Dr. Hudson states this evidence, negative as it is, does not prove that the plankton production in the Passamaquoddy area is not responsible for the transferring of fish into that area. The question of plankton that is brought into the area is an important one. Surveys show that the plankton is relatively scarce where the herring are most abundant. Then is the plankton brought to this area from other points of production utilized so well that it really constitutes a real reason for the presence of these fishes? This brings us back to the old question of the amount of plankton and the reason. From the fisheries standpoint, plankton investigations must, I believe, be brought to a point of perfection where their technique will show not merely a standing crop but total turnover. And because we have no evidence on that subject, the International Commission has had to conclude what was originally guessed: that no prediction as to the result of the construction of these dams could be made.

Dr. Galstoff: I want to call your attention to the observations which I omitted in my talk, devoted to the mineral content of the organisms, as to the source of the organic matter which may be overlooked, and then when you try to balance material available from all known sources with that which goes in solution, that may be really responsible for not giving a balance. We have in the field in Long Island Sound about 40,000 acres of cultivated oyster bottoms; a certain section of it is devoted to our experimental farm and there we do our observation work. The discharge of eggs in that region is

rather concentrated, lasting no more than three or four days for the principal discharge. Having the material on hand when we are measuring the width of the gonads and of the oyster and the weight of the oyster meats every week in summer, and twice a month in the winter, I was able to get some figures not only as to the number of eggs discharged but also as to the weight of the egg and sperm material that is discharged during the spawning season—probably for ten days. These figures were secured in an area of 40,000 acres which extends along fifteen miles in Long Island Sound, where it has an average width of about five miles.

During last year when the spawn was very abundant, there was at least six carloads of mass sperm and eggs discharged into the sea, amounting to about 600,000 pounds. Yet if you make a very careful plankton catch with every available method—pump, net and every other method—you rarely see an oyster egg in the water. As a matter of fact, you rarely see the oyster unless you happen to make your plankton collection at the exact time of the tide. It seems to me this amount of spawn, thrown on a rather limited area is rather significant in the balance of organic matter in sea water.

Dr. Birge: The bottom fauna is a very important element in the food. We have not been able to show or see that the bottom fauna contributed much to this material in solution. There is a big question here which we cut out because we didn't have time to bring it in, and also because we do not know much about it. But we do find this: There are quite a number of lakes that we have studied in which there is a good deal more organic matter in solution than we should expect from the color of the water. If you look at that table closely you will find the higher colored waters have very little organic materials. The lakes which have this large amount are low colored. Largely these lakes are the shallow lakes in the course of a stream, and we suppose there is more material than usual brought in solution from the bottom of such lakes; but if so there is no great amount of material in solution.

So far as the higher plants are concerned, in those northern lakes of ours, if they all went into solution in the water it would be only a very small fraction of a milligram per liter,—too small, in fact, to quote; 0.1 or 0.2 milligrams per liter. And they don't go into solution as a matter of fact but lie on the bottom and come back in decomposition of minor forms. As to the fundamental food for fish and also for the bottom insects as they come up into the water, the bottom material as such does not seem to us to contribute very considerably in the way of quantity. There again, it is guess work, however,—we have no figures on which to base this statement.

Dr. Pearse: There are plenty of lakes in which animals in the open water are using that material.

Dr. Birge: We must be getting from the bottom there a considerable

amount of lower products which have fermented down and decomposed to the point where they do not come into this straight organic compound. There must be from the bottom, of course, large amounts of that sort of material set loose in the water. Our own feeling is that what has been said in regard to the decomposition of peat would probably apply to your organic materials also. As the decomposition goes on the various protein compounds get into a resistant alliance with carbohydrate material and remain for a good while without further decomposition. Whether in that form they are available for higher life is beyond our knowledge. Dr. Waksman worked out in two or three cases the amount of proteins and found 80 per cent in forms that could be used for food. I wish Dr. Krogh would stimulate his European colleagues to go after a matter of this sort.

Dr. Juday: Of course, there are a lot of bacteria growing on the bottom. That problem is now being investigated by our bacteriological department through the influence of our geologists, and they have secured several millions,—some five millions or more—of these bacteria per gram of mud, so that they get very large numbers of bacteria in this bottom material. There is no reason why such bacteria could not serve as food for the higher forms.

OCEANOGRAPHY

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PRESENT TRENDS IN THE INVESTIGATION OF THE RELATIONS OF MARINE ORGANISMS TO THEIR ENVIRONMENT

By T. WAYLAND VAUGHAN

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Introduction

President Powers has paid me the honor of inviting me to contribute to this symposium a paper on some aspect of the relations of marine organisms to their environment. Obviously there was a wide range of subjects from which I might select a topic and I was accordingly perplexed. Since I have recently either published or submitted for publication papers on the ecology of corals and on the application of knowledge of the ecology of marine organisms to deciphering geological history, the two subjects to which I have given most personal attention, they seemed to be eliminated from use on this occasion, but I am using some of my own work as illustrations of some of the topics discussed in this paper. As I have within the past few months made a survey in many countries of the significant current investigations of the relations of marine organisms to their environment, it appeared to me that a succinct summary of the results obtained might be of interest. The study of the development of the present trends has been of keen interest to me and of value in guiding the researches on the biological aspects of oceanography in the institution with which I am connected. Although this development has conformed to the general principles which apply to the advance in research in other fields of science, and consequently much of what I shall say will be as would be expected, there are differences in the details. Those who have not had occasion to follow recent progress in the methods of studying the ocean may not be aware of some important influences that have affected the study of its biological aspects.

Before beginning the account which is to follow, attention should be called to a few important publications which deal with the fundamentals of the problems here considered. Lawrence Henderson has published two most stimulating books, "The Fitness of the Environment,"[1] and "The Order of Nature."[2] The inseparability of an organism from its environment is a thesis which Henderson has developed more elaborately than is possible in the present paper. C. A. F. Pantin is the author of an excellent essay entitled "Physiological adaptation."[3] It appears that the attitude expressed by

[1] Henderson, Lawrence J. The Fitness of the Environment. Pp. 1-317, New York, 1913.
[2] Henderson, Lawrence J. The Order of Nature. Pp. 1-234, Cambridge, 1925.
[3] Pantin, C. A. F. Physiological adaptation. Linnean Soc. Jour.-Zool., vol. 37, no. 256, pp. 705-711, 1932.

me in the present paper is essentially identical with that of Pantin who says:

"Adaptation seems peculiarly evident in the physiological properties of the animal as a whole. These properties are inevitably noticed in any systematic description of the organism in its environment. Their interpretation is necessarily the most complicated, because they involve every character of the organism."

The scope of my discussion is rather narrower than that of Henderson and it is somewhat wider than that of Pantin.

Earlier Investigations of Organisms With Reference to Their Environments

Primitive man recognized that there were air-breathing terrestrial organisms and that there were both fresh-water and salt-water aquatic organisms. But the study of adaptations to the marine environment in general and to the wide variety of different environments within the oceans was necessarily of much later development. The initiation of such investigations is associated with the introduction of the submarine dredge.[4] The Italians Donati and Marsigli began using such dredges for collecting specimens from the sea-bottom before the middle of the 18th century. At later dates dredges were used by O. F. Müller in Denmark in 1799, Henri Milne-Edwards in France in 1830, Edward Forbes in England in 1832, and Michael Sars in Norway in 1835. Forbes was apparently the first to undertake a classification of submarine environments.[5] As a result of his work in the Ægean Sea, he recognized eight depth-zones each characterized by a peculiar assemblage, a community, of animals and of plants where such organisms were present. He attributed much importance to the nature of the bottom. Forbes conjectured that the zero of animal life would probably be found at about 300 fathoms and, accordingly, named the region below that depth as the "azoic" zone. This is a very stimulating article which, although it was published nearly ninety years ago, shows a better grasp of certain aspects of marine ecology than some papers of far more recent date.

It is interesting to read the accounts published by such naturalists as Dana and Darwin about or before the middle of the last century. Both of them were keenly alive to the influence on marine organisms of such factors as temperature, light, depth, and the degree of agitation of the water. The early naturalists were aware of many of the problems presented by the

[4] See Herdman, Sir William, Founder of Oceanography, p. 9, for an account of the influence of the invention of the dredge.

[5] Forbes, E. Report on the Mollusca and Radiata of the Ægean Sea, and on their distribution, considered as bearing on geology. British A.A.S., report of 13th Meeting held at Cork in August, 1843, pp. 130-193, 1844.

adaptations of marine organisms, but, because most of the various tools for scientific research now in common use had not then been sufficiently developed, they were able to make only qualitative observations.

Great advance resulted from the Challenger Expedition, December, 1872, to May, 1876. Murray has given an excellent summary of the more important features of the ocean in their relation to marine organisms in his paper entitled "The general conditions of existence and distribution of marine organisms."[6] This article represents the state of knowledge and opinion regarding such subjects during the period within the twenty years following the termination of the Challenger Expedition. In it Murray gives a brief summary of what was then known regarding the depths of the ocean, the temperatures of the ocean waters, the chemical composition of sea water including the amounts of dissolved gases, the major features of oceanic circulation, and the different kinds of bottom deposits. He discusses pelagic faunas and floras and the difference between such faunas and floras near the shore and those in the open ocean; the relation of organically secreted calcium carbonate to ocean temperatures and depths; the relative abundance of bottom-living organisms according to depth, laying emphasis on the greater number of both species and individuals in the terrigenous deposit near shore; the nature of the food of bottom-living organisms; the relative restriction of the geographic limits of the different kinds of bottom-living organisms; and the similarity between the faunas and floras of high northern and high southern latitudes, and he makes suggestions regarding the means whereby a large proportion of the organisms at present living on the bottom of the sea obtained their distribution.

Murray, in another publication entitled "On the distribution of the pelagic foraminifera on the surface and on the floor of the ocean,"[7] undertook to relate the distribution of pelagic foraminifera both on the surface and the floor of the ocean to the temperature of the surface water. In it he divides the surface of the ocean, according to temperature, into five zones, viz.: two polar zones, one near each pole, in which the annual range of temperature does not exceed 10°F; a tropical zone within which the annual range of temperature does not exceed 10°F; and two temperate zones, one on each side of the tropical zone, in which the annual range of temperature exceeds 10°F. Another article is a classic study entitled "On the temperature of the floor of the ocean and of the surface waters of the ocean."[8] In a fourth publication, his small volume entitled "The Ocean,"[9] Murray published the diagram

[6] Murray, John. Troisième Congr. Internat. Zool., C. R. des Séances, Leyde, 16-21 Septembre, 1895, pp. 99-111, 1896.
[7] Murray, Sir John. Natural Science, vol. 11, no. 65, pp. 17-27, July, 1897.
[8] Murray, Sir John. Geogr. Jour., pp. 1-18, July, 1899.
[9] Murray, Sir John. The Ocean, p. 135, Williams and Norgate, London, 1913.

here reproduced. This diagram illustrates admirably many of the general relations of organisms to different environments in the sea.

With this diagram copied from Sir John Murray, I will bring one stage of the discussion to a close with emphasis on certain facts. The first of these is that Sir John Murray looked upon the ocean as unity in which there is diversity. In that unit, the ocean, he recognized diverse environments. He studied the different types of environments and tried to define them according to physical, and, to some extent, chemical features. Into these environments he endeavored to set the different types of marine faunas and floras. Sir John Murray was an oceanographer, one of the very greatest, and he thought

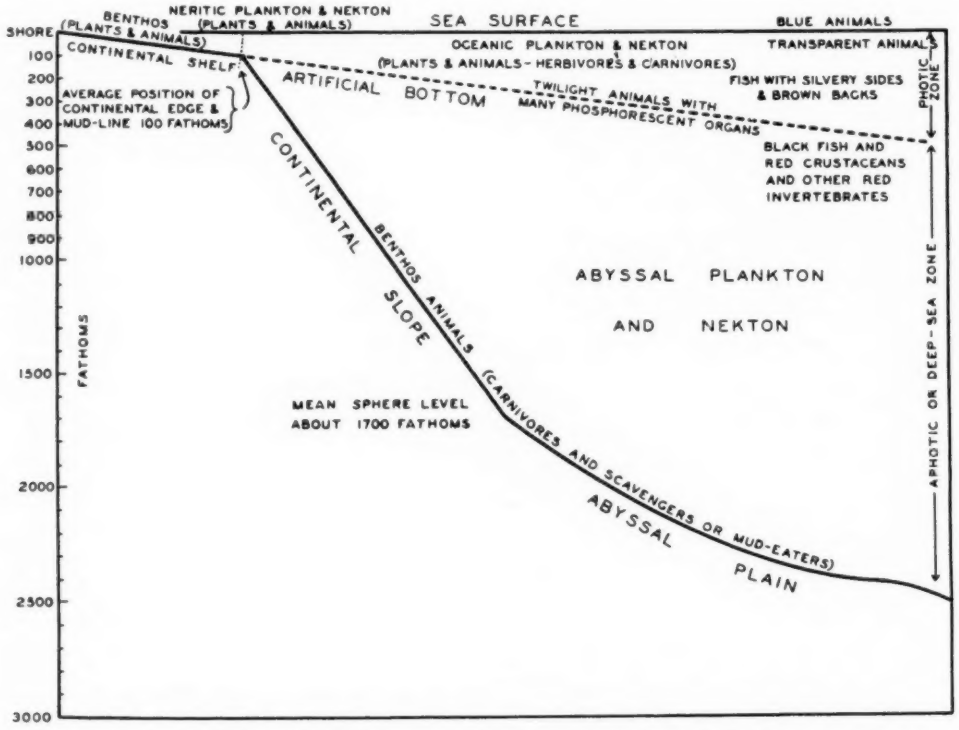

DIAGRAM SHOWING THE OCEANIC FAUNAL AND FLORAL AREAS

in terms of the ocean. It should be noted, however, that his attempts to relate organisms to their environments, with few exceptions, did not include experiments, but his conclusions were based upon observations of the interrelations of the organisms to the conditions under which they live. However, there is ample evidence in his publications that he was aware of the desirability, even the necessity, of experimental work in order to see a little more deeply into relations between organisms and the conditions under which they live.

For another stage in the development of the investigation of the relations between organisms and their environment, I will select as illustrations two of

my own scientific endeavors. Of these, the first is my rather large monograph entitled "Recent Madreporaria of the Hawaiian Islands and Laysan"[10] published twenty-seven years ago. Although the descriptions and illustrations of the coral species occupy a large part of the volume, this paper was intended primarily as a study of the ecology of corals. All available information on temperature, depth, and character of the bottom, was utilized in the definition of the different kinds of environments of the different coral faunas. From this work (pp. 46-47) I will quote three paragraphs, as follows:

"Pressure and diminished light are both correlative with depth. Both factors need further investigation. Another factor that needs study is the food supply; and probably the oxygen content of the water. Some of the factors to which considerable attention has been paid are not considered here, such as position with reference to the lines of the breakers, relations to the fall and rise of the tides, etc.

"As yet comparatively few facts bearing upon the fundamental principles which determine the distribution of corals have been collected. Most authors have contented themselves with merely mentioning the station and depth at which a given form was procured; they usually have not utilized even these data in attempts to discover any underlying principles. We need much more information and more tabulations of the physical surroundings under which the forms, from individuals to genera, have lived; and *a wide range of phenomena should be made the subject of experimental physiological investigation.*" (Not italicized in the original publication.)

"The understanding of the relations of organisms to their physical environment is of the utmost importance to the paleontologist, for it is by the application of such knowledge that he is able to reconstruct the conditions under which organisms now extinct once lived."

My work on the Hawaiian corals was a study of empirical relations, a needed preliminary for more analytical investigations. I recognized and stated the need of experimental work and, accordingly, in 1908 in response to an invitation from Dr. A. G. Mayor, I began an extensive series of experiments on living corals at Tortugas, Florida, and on Andros Island, Bahamas. The general results of these experiments, but not all of the details, have been published in several papers. The experimental investigations included the rearing of corals from the larval stage to ages of as much as five years, the determination of the duration of the larval stage, the rate of growth of the different species under different conditions, their food, and their mechanisms for catching food, the relation of corals to different concentrations of sea salts, the capacity to withstand exposure in the air, their relations to sediment, and crude experiments on their relation to light. Extensive field studies and some experiments were made to determine the interrelation between corals and the movement of ocean water. The experiments on the relation of corals to temperature were conducted by Doctor Mayor himself. These experiments

[10] Vaughan, T. Wayland. Recent Madreporaria of the Hawaiian Islands and Laysan. U. S. Nat. Mus. Bull. 59, 1907.

were the most extensive that had been made up to the time at which they were performed. At the time that the series was brought to its conclusion in 1915, I was aware that all that I had done in most of the experiments was to determine empirical relations for the understanding of which a series of investigations according to the methods of modern physiology was necessary. In one of my papers[11] I have said that it looked as if my most important result was to open a field for further research by others.

In this connection, I shall give the substance of a conversation I had with Professor J. Stanley Gardiner, than whom probably no one has had more field experience with corals. He studied in the field the empirical relations of the corals with which he worked and undertook some experiments. He became convinced that a real understanding of the biological phenomena with which he was dealing required the use of physiological tools and the methods of experimental biology. Accordingly, with the help of his staff and the able collaboration of Dr. James Gray and with the sympathetic support of Professor Joseph Barcroft, he has built up, in connection with the department of zoölogy at Cambridge University, one of the strongest known scientific groups for experimental work on marine organisms.

Another method of attack on the problem of determining the empirical relations of organisms to their environment was developed under the leadership of Dr. W. E. Ritter at the Scripps Institution for Biological Research at La Jolla, California. This method consisted first of the study of the physical conditions in the sea, second, quantitative sampling, third, the interpretation of the data by mathematical treatment.

A statistical inductive method of isolating the effects of the various measured factors and requiring a minimum of restrictions was developed by G. F. McEwen in collaboration with E. L. Michael.[12] An application of this method was made by Michael[13] in an article the title of which is given in the footnote. Along with this investigation McEwen developed methods of estimating statistical significance applicable to the case in which the samples are small, and the distribution is not necessarily normal. The results of this second investigation were rather recently published.[14]. A paper by McEwen dealing with a somewhat similar problem is one entitled "Statistical evidence of the tendency of marine plankton to occur in swarms."[15] The most extensive application of the later mathematical methods developed by

[11] Vaughan, T. Wayland. The oceanographic point of view. Contributions to Marine Biology, pp. 40-56, Sept. 1, 1930.

[12] McEwen, George F., and Michael, Ellis L. The functional relation of one variable to each of a number of correlated variables determined by a method of successive approximation to group averages: A contribution to statistical methods. Amer. Acad. Arts and Sciences Proc., vol. 55, no. 2, pp. 95-133, 1919.

[13] Michael, Ellis L. Effect of upwelling water upon the organic fertility of the sea in the region of southern California. First Pan-Pac. Sci. Conf. Proc., Special Publ., Pt. 2, Bernice P. Bishop Mus., pp. 555-595, 1921.

[14] McEwen, G. F. Methods of estimating the significance of differences in or probabilities of fluctuations due to random sampling. Scripps Inst. of Oceanog. Bull., Tech. Ser., vol. 2, no. 1, pp. 1-137, 1929.

[15] McEwen, G. F. Proc. Fourth Pac. Sci. Cong., Java, pp. 547-548, 1929.

McEwen is in a paper by Esterly, "The periodic occurrence of Copepoda in the marine plankton of two successive years at La Jolla, California."[16] These methods of investigation are undoubtedly valuable and it is safe to say that they will continue to be used in the study of the ecologic relations of marine organisms, but they do not eliminate the necessity for the experimental work to which attention will be paid in a subsequent part of this paper.

The outline which I have given and for which I have selected several illustrations brings to a close the discussion of that phase of the study of marine organisms with reference to the environment, mostly antecedent to the one on which I wish to lay emphasis.

PROGRESS IN THE STUDY OF DYNAMICAL OCEANOGRAPHY AND THE PHYSICAL PROPERTIES OF SEA WATER

The developments within the past few years in the study of organisms with reference to their environment is based on several different kinds of scientific advance. Since we are studying organisms with reference to their environment, the advances that have been made in the investigation of the environment itself should be considered first. It is probable that many biologists do not realize the effect on biological research of recent investigations of the fundamental principles that underlie oceanic circulation. We need to be able to characterize the different water bodies according to their physical and chemical features and to trace the movements of the different water masses. There are several to whom we owe the development of this aspect of oceanography. The first name to be mentioned is that of V. Bjerknes, with whose name should be coupled those of his collaborators, Helland-Hansen and Sandström, and somewhat later Hesselberg and Sverdrup. Much of the methods of modern dynamical oceanography have been developed by Helland-Hansen. To him largely belongs the credit for making possible the practical application of the brilliant theoretical work of Bjerknes. Another man to whom we owe much is V. W. Ekman. This is not the place to review Ekman's work, but his investigations of wind-driven currents and boundary waves are known to everyone familiar with modern oceanographic literature. In this group we should also include the name of George F. McEwen, particularly for his study of upwelling and its rate along the California coast, for his investigations of vertical mixing in the California region, and for the method he has devised for calculating surface drift from differences in surface temperature. To the names of those above mentioned, all of whose work is more or less closely related, should be added those of Merz and his associates and successors, Defant, Wüst, and Lotte Möller, at the Institut für Meereskunde in Berlin. Those whose names are mentioned have laid the foundations for modern dynamical oceanography which are now being so successfully applied in virtually all of the different oceanic basins.

[16] Esterly, C. O. Scripps Inst. of Oceanog. Bull., Tech. Ser., vol. 1, no. 14, pp. 247-345, 1928.

The advances in dynamical oceanography have depended upon the development of more refined technique in the determination of those factors to be utilized in the dynamical treatment of water masses. The invention of the reversing deep-sea thermometer by Negretti and Zambra opened new possibilities for the measurement of sub-surface temperatures in the ocean. Richter improved the original Negretti-Zambra thermometer and he placed inside the protecting tube an auxiliary thermometer which gives the temperature at which the reversed thermometer is read. The method for correcting the reading of the detached mercury column after it was brought on shipboard was devised by Feruglio and incorporated in the equation which bears his name, and it was subsequently improved by Shumacher and others. The deep-sea thermometers have now attained such accuracy that the maximum error should not exceed $\pm$ .01°C, and by increasing the length of the stem to contain the detached mercury the error may be reduced to less than one half that amount. Accompanying the refinement in the measurement of temperatures, there has been refinement in the determination of the density of sea water. The best work on this subject appears to have been recently done in the Physikalisch-Technische Reichsanstalt[17] in Berlin, which undertook the investigations for the Institut für Meereskunde. The determination of density by each of four methods, viz., actual measurement of density, titration for chlorine, measurement of the index of refraction by means of an interferometer, and measurement of the electrical conductivity, has attained the great precision of 10^{-6} in density. The possible degree of precision attained by chlorine titration expressed in salinity is $\pm$ 1 in the third decimal, whereas previously the accuracy was $\pm$ 1 in the second decimal. The significance to biological investigations of these refinements is in being able to trace with greater precision the movement of water masses. It is generally known that the variations in temperature and salinity in the deep waters of the ocean are relatively slight. Therefore, if the movements in the water are to be detected, great precision must be attained in the measurement of temperature and salinity.

Since this paper is addressed to biologists who may not have thought of the interrelations between the circulation of the waters in the oceans and organisms in the sea it may be desirable to give a few illustrations. On subsequent pages mention is made of the upwelling of water along the California coast as the means whereby plant nutrients are brought from lower levels in the sea and thereby replenish the supply in the surface waters which had by the growth of phytoplankton been depleted of plant nutrients. The upwelling is caused by the coastal northerly winds which push the surface water away from the coast to the right of the direction toward which the winds blow, and cause upward movement of water from lower levels to the surface. The

[17] Bein, Willy, Hirsekorn, Heinz-Günther, and Möller, Lotte. Neue Konstantenbestimmungen des Meerwassers. Jour. Cons. Internat. Explor. Mer, vol. 8, no. 1, pp. 48-58, 1933.

water of deeper layers contains large quantities of plant nutrients. The principles that underlie this upwelling are a part of Ekman's theory of wind driven currents. McEwen has put the phenomena for the California coast on a quantitative basis. He has also studied the rate of the upwelling and has found it to range between 27 and 55 meters per month, for the months April to September, inclusive, during which upwelling takes place, the total movement approximating 210 meters. This means that the upwelling water which reaches the surface does not come from great depths but from a maximum depth of about 200 meters during any one season. This estimate has been checked by studying the salinity and temperature characteristics of the different water masses. The biological effect of upwelling is considered in a paper by Michael cited on a previous page, by Moberg, a contributor to this symposium, in some of his studies, and by T. G. Thompson and Grant in their investigation along and off the Washington coast.

As another illustration the distribution of oxygen in the ocean will be taken. Oxygen is introduced into ocean water either from the air or as a result of the photosynthesis of plants. No addition to the supply of oxygen in the water can take place at any level below the level of photosynthesis—below that level there is consumption of oxygen. How does the oxygen obtain its distribution in the deeper waters of the ocean? It is by means of the circulation of the waters, to explain which is the purpose of dynamical oceanography. There is down-sinking of water which is saturated with oxygen in high latitudes and at what is known as the Polar Front. After its down-sinking this water moves and it carries its oxygen with it. In the eastern Pacific there is a sub-surface layer which possesses a very low oxygen content; in the western Pacific there is no parallel to the layer deficient in oxygen of the eastern Pacific. Why? The problem is complex, but a part of the answer is definitely known. There are several areas in the North Pacific for which it has been established that down-sinking of oxygen-laden water takes place. Because of the effect of the rotation of the earth the movement of this water is deflected toward the right and consequently toward the west side of the Pacific basin. Water at similar levels on the east side of the Pacific has been longer cut off from contact with the air than that on the west side.

Movement is prevalent throughout the entire mass of the ocean waters, but there are variations in direction and in rate. The movements transfer from place to place not only floating organisms but also water which possesses definite physical and chemical properties on which the life of the organisms depend.

One of the physical features of sea water which is of great biological importance is the capacity of sea water to absorb or transmit light of different wave lengths. The recent numerous investigations of the penetration of light

into sea water have been made possible by the invention of photo-electric cells which are sensitive to different wave lengths of light. Some of these investigations have been made to determine the depth of penetration of light within specific areas, and other investigations have been made to determine the absorption coefficients of different kinds of sea water for light of different wave lengths. I will merely mention the work of Poole and Atkins at Plymouth, Shelford and Gail at Friday Harbor, Clarke at Woods Hole, Richardson at La Jolla, and Utterback at Friday Harbor. Richardson, in his first series of experiments at La Jolla, undertook to measure from a boat the depths of penetration of those wave lengths between 2900 and 4800 Angström units. His second set of experiments was made in the laboratory on different samples of sea water. For these experiments he used four cells each of which was sensitive to certain definite wave lengths. By using the four cells the range of wave-lengths covered was from 4000 to 8000 Angström units. The results of the latter experiments apply to sea water brought into the laboratory, and, therefore, probably indicate a depth of penetration greater than that actually encountered in the sea. Because of the varying amount of suspended matter in sea water, and also because of variation in the absorption coefficient for light in water of different salinities, there is need to have measurements made in many different regions of the sea and under a wide variety of conditions. The study of this subject by the use of photo-electric cells has yielded important results and we are encouraged to think that we shall soon obtain a still better understanding of this important aspect of the marine environment than we have at present.

DEVELOPMENT OF METHODS FOR THE STUDY OF THE CHEMISTRY OF SEA WATER

We shall now turn attention to the developments in analytical procedure for the determination of those substances, mostly present in small amounts, which either affect the chemical behavior of sea water or which are of significance to marine organisms.

One of the important aspects of the chemistry of sea water has been the study of the factors that control the hydrogen-ion concentration, that is, the buffer system, in sea water. A recent and important publication on this subject is that of a committee appointed by the International Council for the Exploration of the Sea.[18] Several of the investigators of this subject recognized the importance of the accurate determination of the amount of boron in sea water. Recently satisfactory methods for the determination of boron have been devised. It now appears that the buffer system of sea water is adequately understood and satisfactorily formulated in a recent paper by

[18] Buch, K., Harvey, H. W., Wattenberg, H., Gripenberg, S. Über das Kohlensäuresystem in Meerwasser, Internat. Cons. Explor. Mer, Rap. et Proc.-Verb. des Réunions, vol. 79, pp. 70, Sept., 1932.

Buch[19] and in one published in the Bulletin of the Scripps Institution.[20] Apparently we now have a satisfactory solution of the long-perplexing problem, under what condition calcium carbonate may be precipitated or dissolved in sea water.

Methods for the rapid determination of many substances dissolved in sea water were needed. Such methods have been devised for oxygen, silica, calcium, carbon dioxide, phosphate, iron, arsenic, and some other substances. There has been difficulty in the determination of nitrates due to the trouble which has been experienced in getting sufficiently pure chemicals. This subject has recently been reviewed by Cooper,[21] and Atkins[22] has suggested improvements which are intended to obviate the difficulty inherent in the method to which the name of Harvey is attached.

Additional information on the nature and quantity of organic material, that is, carbon compounds, in sea water is needed. Such investigations have been retarded because of the lack of suitable analytical methods. Satisfactory methods have now been devised for the determination of both the organic material in bottom muds and in the water itself.

Concomitant with the advance in the improvement in analytical procedure for the study of sea water, additional information on the vertical and horizontal distribution of the various dissolved gases and plant nutrients has been acquired. One of the recent advances is knowledge of the distribution of oxygen in the Pacific Ocean. The first observations on the deficiency of oxygen at certain levels in the eastern Pacific were made by our lamented friend Johannes Schmidt,[23] but the information on the great areal extent of the water deficient in oxygen resulted from Moberg's[24] work in connection with the expedition of the CARNEGIE and with the work done off La Jolla by the Institution's boat SCRIPPS. On the DANA Expedition in 1929-30 Helge Thomsen made an oxygen section across the Pacific from Panama to New Caledonia.[25] K. Ito has published an article on the oxygen content of sea water in the southwestern part of the North Pacific.[26] Fleming, of the staff of the Scripps Institution, has recently obtained additional information as a result of his work on the United States Naval vessel HANNIBAL off the coasts of Panama and Costa Rica.

[19] Buch, Kurt. Der Borsäuregehalt des Meerwassers und seine Bedeutung bei der Berechnung des Kohlensäuresystems im Meerwasser. Internat. Cons. Explor. Mer, Rap. et Proc.-Verb. des Réunions, vol. 85, pp. 71-75, 1933.

[20] Moberg, Erik G., Greenberg, David M., Revelle, Roger, and Allen, Esther C. The buffer mechanism of sea water. Scripps Inst. Bull., Tech. Ser., vol. 3, no. 11, pp. 231-278, June, 1934.

[21] Cooper, L. H. N. The determination of nitrate in the sea by means of reduced strychnine. Mar. Biol. Asso. Jour., vol. 18, pp. 161-166, 1932-33.

[22] Atkins, W. R. G. Nitrate in sea water and its estimation by means of diphenylbenzidine. Mar. Biol. Asso. Jour., vol. 18, pp. 167-192, 1932-33.

[23] Schmidt, Johannes. On the contents of oxygen in the ocean on both sides of Panama. Science, pp. 592-593, June 5, 1925.

[24] Moberg, E. G. Distribution of oxygen in the Pacific. Contributions to Marine Biology, Stanford Univ. Press, pp. 69-78, Sept. 1, 1930. See also, Moberg, E. G., and Graham, H. W. The distribution of dissolved oxygen in the sea according to the investigations of the CARNEGIE. In press as one of the reports on the CARNEGIE Expedition.

[25] Thomsen, Helge. Oxygen in the tropical Pacific. Nature, Mar. 21 and 28, 1931.

[26] K. Ito. Oxygen-gas content of sea water in the southwestern portions of the North Pacific. Records of Oceanog. Works in Japan, vol. 2, no. 2, pp. 82-91, 1930.

There is in the eastern Pacific, usually between depths of about 600 and 1200 meters, a layer in which the oxygen declines to less than 0.5 ml per 1, that is, to 5% or less of complete saturation. What influence has this layer on the vertical distribution of organisms? Prior to the discovery of this condition in the eastern Pacific, except preliminary observations by A. Agassiz in 1891-92, it seems that no one had attempted to make an investigation of the kinds and the relative quantities of organisms found at different levels in the deeper layers below the surface. Already some preliminary work has been done on this subject by the Scripps Institution but the results are as yet only suggestive. This discovery makes it important to get more information on the capacity of marine organisms to live at low oxygen tensions, and it has revealed problems that will probably require long-continued investigation. The recent summary article on oxygen consumption and oxygen tension by Pei-Sung Tang[27] is pertinent in this connection. That conditions in the western Pacific are very different from those in the eastern Pacific is shown in the papers by Thomsen[25] and Ito.[26]

The advances in dynamical oceanography and in analytical chemical procedure, coupled with the results obtained on numerous expeditions, have given us a new picture of the physico-chemical conditions in the sea and of the transport of substances and properties of biological significance. Accordingly, we now need to consider problems of adaptation of which we were not aware only a few years ago.

PHYSIOLOGICAL INVESTIGATION OF MARINE ORGANISMS

The developments of methods for studying the physical and chemical features of the ocean have followed, and have been largely dependent on advances in theoretical chemistry, particularly physical chemistry. There has also been progress in bio-chemistry and bio-physics and in the application of such knowledge to understanding the activities of living organisms. Although such subjects are matters of common knowledge among modern biologists, it is necessary for the purposes of this review to mention a number of the fundamental vital processes to be investigated in studying the adaptations of marine organisms.

The most striking difference between terrestrial and aquatic organisms is that the former live in air, a gaseous, and the latter in water, a liquid external medium. Air consists roughly of one-fifth oxygen and four-fifths nitrogen, i.e., one liter of air contains approximately 200 ml of oxygen. The amount of oxygen in sea water varies with the temperature and salinity and, accordingly, ranges between 4.6 and 8 ml per liter when there is complete saturation. Consequently, the amount of oxygen in sea water per unit volume is, when saturated, approximately between 1/25 and 1/43 of the amount in the air.

[27] Tang, Pei-Sung. On the rate of oxygen consumption by tissues and lower organisms as a function of oxygen tension. The Quarterly Review of Biol., vol. 8, no. 3, pp. 260-274, 1933.

The respiratory arrangements of terrestrial and aquatic organisms, therefore, must differ. Furthermore, terrestrial organisms, in order to preserve an internal medium in a constant or nearly constant state, must have protective coverings, while such coverings are not needed to nearly such a degree in most aquatic organisms.

The most salient difference between those aquatic organisms that live in fresh water and those that live in salt water is that in general there is a greater difference between the salt concentration in the body fluids of the fresh water organisms and that of their external medium than there is between the salt concentration in the body fluids of marine organisms and that of the medium in which they live. It is also known that many species of marine organisms are often subjected to considerable variations in the salt concentration in the aqueous medium in which they live. This would suggest that in the study of the adaptation of marine organisms one of the first subjects to be investigated would be the relation between the composition of their body fluids and the composition of the medium in which they live. This is a subject to which attention is being paid by many physiologists and biophysicists and it forms a part of the research program of nearly every, if not every, oceanographic institution in the world. A list of the researches which have been conducted within the past few years or which are now underway would be a formidable one. Under these circumstances only a few samples can be given. The first sample will be a summary paper by Pantin[28] on the origin and composition of body fluids, to which a considerable bibliography is attached.

A successful recent investigation is the study by A. B. Keys[29] of osmotic regulation in the eel, conducted in Professor Krogh's laboratory in Copenhagen and Professor Barcroft's laboratory in Cambridge. I mention these papers by Keys because von Buddenbrock[30] says in a recent publication:

"On the contrary one can maintain with some probability that the gills of this animal [*Carcinus maenas*] perform osmotic-regulatory work.

"On the basis of this work one can probably in the future also answer the question how marine fishes regulate their water budget, a question for which, although it is so pertinent, no one has yet found a definite solution."

The final sentence in the second paper by Keys reads as follows:

"The kidney conservation of salt and elimination of large amounts of water is shared with the stenohaline fresh-water fishes; the elimination of excess salt and conservation of water by the gills appears to be common to the stenohaline marine teleosts and the euryhaline forms like the eel."

[28] Pantin, C. F. A. The origin of the composition of the body fluids in animals. Biol. Reviews, vol. 6, no. 4, pp. 459-482, 1931.

[29] Keys, A. B. The heart-gill preparation of the eel and its perfusion for the study of a natural membrane in situ. Zeitsch. vergleich. Physiol., Zeitsch. wissenschaft. Biol., Abt. C, vol. 15, no. 2, 1931; The mechanism of adaptation to varying salinity in the common eel and the general problem of osmotic regulation in fishes. Royal Soc. Proc., B, vol. 112, pp. 184-199, 1933.

[30] von Buddenbrock, W. Die für die D. W. K. 1928-1929 durchgeführten Arbeiten. Die Arbeiten der Deutsch. wissenschaft. Komm. für Meeresforschung, 1926-1929, der Deutsch. wissenschaft. Komm. für Meeresforschung, Ber. neue Folge, vol. 5, no. 4, p. 224, 1930.

Keys has shown that work is performed by the gills in the regulation of the water budget in fishes and that the thinking of many students of osmotic regulation prior to von Buddenbrock and of von Buddenbrock himself was correct.

In addition to fishes, a wide range of marine invertebrates is now being subjected to careful investigation, as is shown in the papers by von Buddenbrock and by Pantin to which reference has been made. H. Delaunay[31] has published the results of a valuable series of researches on the nitrogenous excretion of marine invertebrates. Only the last number of this series of investigations is cited, for in it references are made to the earlier numbers of the series and it contains a summary, the general conclusions, and a bibliography. Other work which will merely be mentioned in passing is the experiments on several marine invertebrates being conducted by Fox at the Scripps Institution.

It may only be intimated that numerous investigators have been considering the relation between the salt concentrations in the fluids within plant cells and the concentration of salts in the surrounding water. In this connection, the problem also arises as to how certain cells of both plants and animals are able to select substances of which only small amounts are in solution in sea water and accumulate substances, such as iodine, potassium, and metals, within themselves so that they attain a concentration very much greater than that in the water from which the substances are taken.

Another subject of great importance is that of the cycle of organic matter and plant nutrients in solution in sea water or present in the bottom deposits of the sea. I am not certain just when critical investigations of the nitrogen cycle in the sea were first undertaken, but as Brandt was active in such researches years ago it is probable that he is their father. The origin and history of the nitrogen compounds in the sea are now being studied in connection with the bacteriological programs at all important oceanographic institutions. Since Dr. Waksman is to present a paper on bacteria in the sea as a part of the program of this meeting, I will merely say that such investigations are of great significance for understanding both the biological and chemical features of the sea, and that they form a part of the program of each of the three oceanographic institutions in the United States.

Coincident with the study of the nitrogen cycle, and other cycles, and the distribution of the plant nutrients in the sea have gone numerous experimental investigations of the physiology of phytoplankton. In these researches many investigators have played an honorable rôle. Among the leaders is our friend Gran, with whom T. G. Thompson has done valuable work in Puget Sound. There are the outstanding experiments of Marshall and Orr and the beautiful series of experiments conducted by Schreiber in

[31] Delaunay, H. Recherches biochimiques sur l'excrétion azotée des invertébrés. Station Biologique d'Arcachon, Bull., vol. 24, pp. 95-214, 1927.

Helgoland. A vigorous growth of phytoplankton depletes the water of its plant nutrients. The means of the replenishment of the plant nutrients have been investigated in many places. In certain localities it has been ascertained that the replenishment results from the overturn of the water due to the surface cooling during the colder part of the year, for instance, in the vicinity of Plymouth and in the coastal waters of northern Europe. In other places the replenishment seems to be caused by upwelling of water from deeper layers, as along the west coast of Africa and the west coast of the United States from Washington to southern California. There is also evidence of such upwelling in the Gulf of Panama and along much of the west coast of South America.

The influence of light on the growth of phytoplankton is being studied in many places. It has been largely for the purpose of understanding the depth to which photosynthesis is active that investigations have been made of the depth of penetration of light of different wave lengths into sea water. Notwithstanding the advances which have been made during the past few years in studying the factors which influence the occurrence and growth of marine plants in the ocean, the investigation of the subject is still only in a preliminary stage. We still need critical studies of the effects of light of different wave lengths and different intensities. The Smithsonian Institution's Division of Radiation and Organisms, under F. S. Brackett, is setting a good example for such researches.

One of the other lines of the investigation of marine organisms with reference to their environment is the study of the oxygen relations. The President of our Society is one of the leaders in this kind of research. The Woods Hole Oceanographic Institution is fortunate in having as a member of its staff Redfield, one of the masters in this particular field of research. We need to know the oxygen requirements of the different marine organisms and the mechanisms which these organisms possess for oxygen capture. The surface waters of the ocean are in general supersaturated with reference to oxygen. Out to the limit of the continental shelf off the different shores the water on the bottom of the ocean is undersaturated in oxygen, a condition shown by the prevalence of reduction. The water layer in the eastern Pacific in which there is a great oxygen deficiency has already been mentioned. In the eastern Pacific in general, the maximum percentage of saturation of the water below the minimum layer usually ranges between 30% and 40%. The bottom waters of the Atlantic contain more oxygen than those of the Pacific, the degree of saturation being about 75%. Organisms live in regions in which oxygen is plentiful and also in regions in which the oxygen supply is small. What are the differences in the adaptation of the different marine organisms to the different quantities of oxygen available for their vital activities? Reference has already been made[17] to the paper

by Pei-Sung Tang, "On the rate of oxygen consumption by tissues and lower organisms as a function of oxygen tension." This subject is also one which is being studied at many different places.

Another aspect of the relations of organisms in the sea comprises what they swallow in order to get their food and their capacity to digest substances that they ingest. The food of commercial fishes is investigated in connection with all fisheries services and also by others interested in problems of digestion. C. M. Yonge[32] has recently published a paper entitled "Digestive processes in marine invertebrates and fishes" in which he covers the field indicated by the title. H. Sandon[33] is the author of a volume entitled "The food of Protozoa." As these two memoirs bring the subjects with which they deal almost up to date, only a few comments are needed here. In the present work on the food and digestion of marine organisms attention is paid to the digestive enzymes with reference to the kinds of food substances that the organisms can digest. Many organisms do not select before ingestion from the material that they swallow the substances that they can digest. The selection is made by the digestive fluids after ingestion, the indigestible part of the material being eliminated. Yonge in the article by him here cited says (page 204):

"Undoubtedly the point of greatest practical importance is the specialization of digestive enzymes. It is clearly useless to expect an animal to obtain nourishment from material which it cannot digest owing to lack of the necessary enzymes."

Very recently Yonge has studied the digestive enzymes of molluscs and corals, Marshall and Orr at Millport are studying those of copepods, and Fox and Marks at the Scripps Institution are studying those of molluscs, especially *Mytilus californianus*, and other marine invertebrates. Myers at the Scripps Institution has been paying attention to the food of foraminifera, but without studying the digestive enzymes.

Another factor on which we need information in order to understand the relations of organisms is the effects of temperature. Temperature experiments have been made on many organisms, but I will confine these remarks to those that have been made on corals. Such experiments have been conducted by A. G. Mayor and C. H. Edmondson. As Edmondson's paper is of more recent date than Mayor's and as it contains references to Mayor's work, I will refer only to it.[34] The first paragraph in Edmondson's account of his experiments on increasing temperature reads as follows:

"After learning the temperature conditions under which the corals of Waikiki reef normally exist and the thermal variations to which they are usually subjected, it seemed desirable to determine their comparative re-

[32] Yonge, C. M. Jour. Cons. Internat. Explor. Mer, vol. 6, no. 2, pp. 175-212, 1931.
[33] Sandon, H. Publications of the Faculty of Science, Egyptian University, no. 1, pp. 187, 1932.
[34] Edmondson, Charles Howard. The ecology of an Hawaiian coral reef. Bernice P. Bishop Museum Bull., 45, 1928.

sistance to increasing and decreasing temperatures even to the extreme levels of their endurance. In testing the resistance to rising temperatures, three forms of laboratory experiments were employed. In one set of experiments the sea water in a shallow container in which the corals were placed was raised, usually by electricity, to the temperature desired and maintained at that degree for definite periods. At regular intervals specimens of corals were removed and placed in a strong current of sea water and their condition determined on the following day or at some later period."

The first paragraph of his experiments on resistance to decreasing temperature reads as follows:

"That living organisms are more capable of enduring a gradual reduction of temperature than a gradual increase of temperature is well known. Pfeffer (20) says: 'It is easy to understand that, owing to the depressant effect of low temperatures upon metabolism, they should take longer to produce a fatal effect than high ones, which steadily accelerate respiration'."

Edmondson also studied experimentally the range of the temperature endurance of planulae and the effect of temperature on feeding responses. The results of such studies as those conducted by Mayor and Edmondson give information on the temperature limits that species of adult corals will endure, and also the results of the effect of temperature both above and below normal on such essential activities as the capture of food. Since many marine organisms attain their wide geographic distribution by means of floating larvae, it is necessary to have investigations made of the temperature limits that the larvae will endure. Edmondson has given us information on this subject for the Hawaiian corals, and for his results we are grateful. Such investigations should be extended not only to the corals of other regions but to all of those groups of organisms that have floating larval stages.

Light is an important factor in influencing the distribution of marine animals in addition to the rôle that it plays in the photosynthesis of marine plants. Many studies of its influence have already been made but, as is the case with the study of other factors that affect marine organisms, the investigations have not yet been sufficiently extensive. A note has already been made on my own crude experiments on the possible influence of light and the exclusion of light on corals. More satisfactory experiments were conducted by C. M. Yonge.[35] A study of Esterly[36] on the copepods at La Jolla represents an attempt to ascertain the interrelation between light and the abundance of copepods at the surface by using a statistical method invented by McEwen. There have been numerous other recent investigations, but of these only the one by Spooner[37] at Plymouth, will be cited. Although Doctor Clarke will pay attention to this subject in this symposium, I wish in the

[35] Yonge, C. M., and Nicholls, A. G. The effect of starvation in light and in darkness on the relationship between corals and zooxanthellae. Great Barrier Reef Exped. 1928-29, Scientific Repts., vol. 1, no. 7, 1931.

[36] See no. 16 above.

[37] Spooner, G. M. Observations on the reactions of marine plankton to light. Mar. Biol. Asso. Jour., new series, vol. 19, no. 1, pp. 385-438, 1933.

present connection to emphasize the importance of such researches in understanding the ecologic relations of marine organisms.

The relation of marine fishes to the color of the background and the changes that take place in the color of fishes with reference to background is a subject which is intimately related to the effects of light. Two recent papers on this subject are, one by F. B. Sumner entitled, "The differing effects of different parts of the visual field upon the chromatophore responses of fishes,"[38] and another by Sumner and Fox, both of the staff of the Scripps Institution, entitled, "A study of variations in the amount of yellow pigment (xanthophyll) in certain fishes, and of the possible effects upon this of colored backgrounds."[39] Sumner has submitted for inclusion in the memorial volume to James Johnstone, being published as the Annual Report of the Lancashire Seafisheries for the year 1933, an article entitled, "Studies of the mechanism of color changes in fishes," in which he has endeavored to bring up to date the entire subject of the color changes of fishes with reference to background. Because of its bearing on the papers just mentioned, a note recently published in *Science* entitled "Expansion and contraction of chromatophores," by S. O. Mast[40] will be cited. Mast says:

"It is well known that the colored substance in the chromatophores in the vertebrates is in the form of numerous discrete granules and that these granules move on definite paths through the cytoplasm out into the various branches of the chromatophores under certain conditions, and on the same paths back into the central part under other conditions."

The point to which I wish to call attention in the article by Mast is that in it is said that although much is known regarding the empirical behavior of the colored granules in the chromatophores, it appears that the actual mechanics of the processes involved are not yet understood. The last sentence in Mast's article contains the words "until more is known about the mechanics of the processes involved." From the statements above made it is clear that the investigation of the color changes in fishes has not yet been brought to a satisfactory conclusion. There are other animals besides fishes that need to be studied with reference to color changes.

Reproductive Cycles and Life Histories

Another topic to be considered is that of the reproductive cycle in marine organisms. Because of its commercial significance the oyster is a classic object for such research. Only the recent work of Galtsoff and Coe in the United States, and Amemiya in Japan will be mentioned. Coe has recently published a paper entitled, "Season of attachment and rate of growth of sedentary marine organisms at the pier of the Scripps Institution of Ocean-

[38] Sumner, F. B. Biol. Bull., vol. 65, no. 2, pp. 266-82, 1933.
[39] Sumner, F. B., and Fox, D. L., J. Exp. Zool., vol. 66, no. 2, pp. 263-301, 1933.
[40] Mast, S. O. Expansion and contraction of chromatophores. *Science*. New series, vol. 78, no. 2028, pp. 435-6, 1933.

ography, La Jolla, California."[41] In this paper he considers the algae and representatives of a large number of groups of invertebrates found on the Scripps Institution's pier. The work of Galtsoff, Amemiya, and Coe, mentioned as illustrations, represents a greatly needed kind of research, and it is fortunate that such investigations are being prosecuted in many places.

A subject of much significance to general marine biology and for several different groups of organisms of special importance for geologists is the life history of marine organisms. In my presidential address before the Paleontological Society in December, 1923, I said:

"Most of the marine organisms which are available for use in geologic correlation are either sedentary or move very slowly in their adult life. This statement applies to most of the Foraminifera, corals, echinoids, most Bryozoa, and most mollusks. The members of at least several of these groups of organisms, however, pass through free-swimming larval stages, and, as the major agency that will cause dispersal is ocean currents, it is of vital importance to know both the duration of the free-swimming larval stage of members of each group of organisms and the system of ocean currents of each geologic epoch. Unfortunately, information on both of these subjects is meager."[42]

It is probable that more attention has been paid to the early stages in the life of commercially important fishes than to any other one group of marine organisms. For many of the species every stage from the egg to the adult is known. Furthermore, the eggs and the larvae of some fishes have been subjected to laboratory experiments to ascertain the limiting conditions of hatching and of life during the larval stage. As regards the marine invertebrates, ten years ago at the time I prepared the presidential address from which a quotation has been made, I did not undertake to go through the literature and compile what was known regarding the life histories of each of the groups of marine invertebrates mentioned above, but I went to my friends who were specialists on the different groups, and the results of my inquiries were disappointing. At present several investigations of significance are under way. At the Scripps Institution E. H. Myers has been working on the life histories of several of the local species of foraminifera and he has succeeded in rearing sexually-produced individuals in two species, *Patellina corrugata* and *Spirillina vivipara*. He has also reared asexually-produced individuals in each of seven different species, but the asexual generation of species of foraminifera had been previously reared by other workers. For corals we have my work in 1910 and Edmondson's later studies. Both Edmondson and I undertook to ascertain the duration of the free-swimming larval stages in the species of corals that we studied. Miss Lebour at Plymouth is conducting culture experiments on the larval stages of a number

[41] Coe, W. R. Scripps Inst. Oceanog. Bull., Tech. Ser., vol. 3, no. 3, pp. 37-86, 1932.
[42] Vaughan, T. W. Criteria and status of correlation and classification of tertiary deposits. Geolog. Soc. Amer. Bull., vol. 35, no. 4, pp. 677-742, 1924.

of species of gastropods and has already published at least seven papers. J. Risbec[43] is the author of a paper entitled "Notes sur la reproduction de quelques Prosobranches néo-calédoniens" in which he describes the larval forms of eight different species of molluscs found in New Caledonia. Marshall and Orr have been studying the life history of copepods and a considerable amount of other work has been done on that group.

Diseases of Marine Organisms

Another topic to which more attention needs to be paid is that of the diseases of marine organisms, a subject on which there were nine papers on the program of the Fifth Pacific Science Congress in Vancouver last June (1933). The titles of two papers were "Recent advances in our knowledge of epidemic diseases among fish in the countries bordering the Pacific," by H. S. Davis of the United States Bureau of Fisheries and "Economic aspects of parasitism and epidemic diseases among fish" by H. B. Ward of the University of Illinois. Recently we have had at the Scripps Institution a dramatic and disconcerting instance of a fish disease. N. A. Wells has for some time been conducting experiments on the oxygen consumption of the local species of killifish, *Fundulus parvipinnis,* at different controlled temperatures. Suddenly a disease began to affect his stock of specimens and interrupted his experiments for several months. Wells and the Institution's bacteriologist, C. E. ZoBell, undertook a study of the cause of the disease and now definitely know the causative organism. It appears that the disease was hitherto entirely unknown and that Wells and ZoBell have been able to give a complete account of it, at least in so far as it affects *Fundulus parvipinnis.* The same disease affects another species of fish, *Atherinops affinis,* locally called "bay smelt." Does this disease also affect the local species of sardine, *Sardinea caerulea?* This disease may be an important factor in the life of the local fishes. These notes merely direct attention to a field of research which is of significance as regards certain organisms that live in the sea and one which may yield results of value in the investigation of economic fishes.

Summary of Methods and Subjects in the Study of Adaptation

In studying the adaptations of marine organisms there are at least four different methods, as follows:

1. The study of organic communities, the physical and chemical conditions under which the communities exist, the constituents of the communities, and the interaction between the different members of the communities.
2. The study of a large group or phylum with reference to the activities and the special adaptations of members of that group to different types of environment.

[43] Risbec, J. Inst. Océanographique, Ann., nouvelle série, vol. 10, pp. 23-33, 1931.

3. The comprehensive study of a single species with reference to its activities and special adaptations, or such a study of a small group of closely related species.
4. The comparative study of a single function, such as osmotic relations, respiration, or digestion in a wide range of organisms, or a study of responses to particular stimuli such as light and changes in temperature.

Each of these methods is good, and investigations are now in progress according to each of them.

In the foregoing paragraphs I have paid brief attention to subjects that need to be considered in the study of the adaptation of marine organisms, as follows: the composition of body fluids and osmotic relations, the cycles in the sea of chemical substances of biological significance, the physiology of phytoplankton, respiration, food and digestion, effects of temperature changes and light, color changes with reference to background, reproductive cycles, life histories, and diseases. This list is not intended to be complete, it is rather a series of samples. Its purpose is to show that now we have available for use a wide range of physical and chemical tools by means of which we can make more refined analyses of the physical and chemical features of the external environment than was hitherto possible, and that, by the use of the same tools or of tools developed upon the same basic principles, we can also ascertain the life processes of the organisms that we are trying to understand. It is this more extensive and more intensive use of physical and chemical tools, accompanied by the introduction of controlled laboratory experimentation, that characterizes the difference between the present researches and the earlier researches on the adaptation of marine organisms to their environment. These trends have developed slowly during a number of years and they belong to no one country.

CONCLUSIONS

a. If marine organisms are to be studied for the purpose of understanding their relations to their environment, the factors in the environment that affect the organisms must be known before the effect of such factors can be ascertained. The student of the ecology of marine organisms must, therefore, know the physical and chemical features of sea water and the history and variations of those features.

b. In the early stages of the investigation of marine organisms attention was logically directed to the taxonomic enumeration of species and the classification of the organisms with reference to the more obvious features of the environment. The work of Forbes belongs to this category.

c. Later a wider range of phenomena was taken into consideration, as is illustrated by the diagram copied from Sir John Murray. Much of the work of Stanley Gardiner and of myself on corals belongs to this category.

d. Gradually experimental methods were developed and introduced, but the first experiments did not extend beyond attempts to ascertain empirical relations. However, it was immediately recognized by those engaged in such investigations that the further analysis of the phenomena being studied required controlled laboratory conditions and the use of biophysical and biochemical tools. This completed the preparation for the present stage of our researches.

e. Now the aim is to understand organisms as dynamic entities. Dynamic processes are operative within every organism, from the lowest to the highest, and between the organism and its environment there is action and reaction—if the organism is to survive it is inseparable from its environment.

f. But in trying to achieve our end we should not lose sight of a number of important facts. There is within the organism not a single organ, but a number of organs and these organs constitute an entity, which is a unit. We cannot understand the function of a part, unless we know the relations of the part to the whole.

g. In our studies of organisms through the application of biophysics and biochemistry in the laboratory let us not forget that what we are trying to understand is something that is happening in the waters of the ocean. The problems now before us were revealed by observation and the recognition of empirical relations. Not all empirical relations have yet been discovered. We must continue to study and collect in the ocean. With the ocean we must preserve intimacy for it is the source of our problems and from it we draw our inspiration.

THE DISTRIBUTION AND CONDITIONS OF EXISTENCE OF BACTERIA IN THE SEA[1]

By SELMAN A. WAKSMAN

(From the Woods Hole Oceanographic Institution and New Jersey Agricultural Experiment Station)

Bacterial Population in the Sea

The two major processes with which the bacteria in the sea are chiefly concerned are the decomposition of plant and animal residues and the transformation of certain simple elements and compounds. These processes result in the mineralization of the complex organic substances and in the liberation of the elements which are essential for the nutrition of the marine diatoms and algae in an available form. But in addition to the processes of decomposition and transformation, the marine bacteria can also serve as food for marine animals, hence their synthetic activities may be of considerable importance. Our knowledge of the extent of bacterial synthesis in the sea is still very limited; although it has been suggested (7) that the bacteria in the sea are capable of developing at the expense of the dissolved organic matter, Krogh (8) obtained evidence to show that only a small part of this organic matter is available for bacterial growth. Our knowledge of the bacteria capable of causing diseases of plants and animals in the sea is also limited. One must emphasize, therefore, for the present only the first two processes, in which the bacteria were shown to take an active, if not a predominant part, and the importance of which in the cycle of life in the sea cannot be overemphasized.

Morphologically, the marine bacteria belong to the rod-shaped forms, cocci and spirilli, the last group comprising both coma-shaped and true spiral-forming organisms. Although the majority of the bacteria so far isolated from sea water are aerobic in nature, many anaerobic forms are also found to occur in the sea, especially in the bottom material. Physiologically, the marine bacteria can be divided into autotrophic and heterotrophic forms. The first group comprises those bacteria which are capable of synthesizing their cell substance out of chemical elements, or simple inorganic compounds, utilizing the energy liberated by the oxidation processes; however, these bacteria occupy in the sea a secondary place, both in abundance and in the variety of activities, although they are chiefly responsible for certain important processes, such as nitrification and sulfur oxidation. The heterotrophic bacteria are more important both numerically and due to the greater variety of their activities in the sea; they are usually found in close association with the organic substances in the sea, comprising both the residues

[1] Contribution No. 39 of the Woods Hole Oceanographic Institution and Journal Series Paper of the New Jersey Agricultural Experiment Station, Department of Soil Microbiology.

of the dead plants and animals and the living forms, as well as with the organic matter in the sea bottom, namely the marine humus.

One may consider the sea as consisting of three centers or loci of bacterial life: 1. The marine plankton, with unequal distribution of the bacteria within the animal and plant plankton. 2. The marine bottom, with a marked difference in the abundance of bacteria in the sand and mud bottoms. 3. The sea water itself, which represents, however, only a poor medium for bacterial development, as compared with the other two loci; whether this is due to the limited availability of the dissolved organic matter in the sea water or to some other factor, still remains to be determined.

METHODS OF STUDYING MARINE BACTERIA

In considering the distribution of bacteria in any natural substrate, it is essential to discuss first the methods used in measuring the abundance of these organisms. Just as in the study of the bacteria in the soil, three distinct methods are made use of in the study of marine bacteria: 1. The plate culture method, whereby the material itself or a definite suspension of it in water is mixed with a favorable gelatin or agar medium and the colonies formed by the bacteria on this medium, after a certain period of incubation, counted. 2. The direct microscopic method: the bacteria in sea water must first be concentrated by filtration or by centrifuging; however, in the case of the plankton or bottom material this is not necessary, since the number of bacteria is high enough and they can be counted directly. 3. The elective culture method, largely used for demonstrating the occurrence and abundance of certain specific groups of bacteria in the sea. Another method was recently introduced, which is a combination of the last two; it consists in suspending glass slides in sea water or burying them in the bottom material; the bacteria will accumulate on the slide; they are then stained and examined. These different methods have each certain distinct advantages as well as limitations. A proper combination of these methods will result in a fair representative picture of the bacterial population of the sea.

DISTRIBUTION OF BACTERIA IN SEA WATER

The numbers of bacteria found in sea water, as determined by the plate method, are ordinarily reported to range from very few cells to hundreds of thousands of cells in 1 cubic centimeter of water. The lower figure is usually found in the case of water taken at some distance from shore, while the higher figures are reported for water taken near shore, especially at the mouth of drainage canals, sewage outlets, etc. The distance from shore, the depth of water, the nature of the bottom material, and various other factors, have been shown to exert a decided influence upon the numbers of bacteria. Russell (13), for example, has shown that the water in the Bay of Naples con-

tained 5 to 120 bacteria per cubic centimeter; the bacteria were evenly distributed at the various depths of water. Fisher (5) found the bacterial numbers to range from 0 to 29,400 bacterial cells in 1 cc. of water. The numbers were highest at the edges of ocean streams, where they came in contact with other masses of water differing in physical nature; these high numbers were believed to be due either, 1. to masses of plankton organisms which tend to die off at such edges of water streams, or 2. to a vertical mixing of the waters at the contact of the two currents, which result in the carrying of the bacteria from the lower depths upwards. Many of the samples, especially those containing the larger numbers of bacteria, could hardly be considered as representing typical water samples, since they were taken either too close to shore or were found to contain abundant algal material.

According to Drew (4), water near Andros Island contained about 15,000 bacterial cells per 1 cubic centimeter, to a depth of 500 to 700 meters, while below that layer only about 20 bacteria were found in the same quantity of water; this marked difference was explained by the fact that the upper layer of water originated locally, while the lower levels came from the deep ocean. In a recent study of the abundance of bacteria in the Clyde Sea area, Lloyd (10) found that the surface water was richest in bacteria, the numbers diminishing with depth, then increasing again at the bottom; at the surface, the numbers of bacteria fluctuated markedly, without any noticeable seasonal trend, while below the surface the numbers were more or less constant; the bacterial numbers fluctuated widely throughout the day in the surface layers, but the fluctuation was only limited at the lower depths of water.

The larger numbers of bacteria usually observed along the shore is no doubt due to the higher organic matter content, as a result of the richer plant and animal life near shore; it is not due, however, to any great extent, to the washing in of bacteria from land. Reuszer (12) reported that sea water in shallow regions, where the water tends to be mixed from top to bottom, contains much larger numbers of bacteria. This can be correlated with the greater plankton development and the greater amount of organic matter made available to the bacteria.

DISTRIBUTION OF BACTERIA IN THE SEA BOTTOM

The numbers of bacteria in the marine bottom exceed very considerably those present in the water itself. Russell (14) found that mud bottoms, at depths of water less than 200 meters, contained 70,000 to 285,000 bacteria in 1 cubic centimeter of mud, the numbers decreasing with distance from land. At greater depths of water, the numbers diminished, namely to 12,000—27,000 in 1 cubic centimeter of mud, these numbers then remaining more or less constant. The mud in the neighborhood of Woods Hole contained fewer bacteria than that of the Bay of Naples, which was correlated with

the lower temperature of the former. Most of the bacteria present in the mud were shown to be characteristic of this particular habitat. Drew (4) found in the mud off Andros Island as many as 160,000,000 bacteria per 1 cubic centimeter. Similar results were obtained by Smith (15), Lipman (9) and Bavendamm (1). Lloyd (11) observed for the Clyde Sea area a certain bacterial zonation in the mud correlated with the mud stratification; the surface layer of mud contained up to 300,000 bacteria in 1 gram of dry mud, the numbers diminishing with depth. According to Reuszer (12), the horizontal distribution of bacteria in the extreme surface layer of mud is independent of the amount of organic matter present in the mud but is largely dependent upon the degree of its decomposition; below the surface layers of mud, the distribution of bacteria is directly correlated with the organic matter content. The bacterial numbers on the continental shelf were found to decrease regularly with distance from land; however, in the deeper layers of mud, the numbers remained constant.

Samples of bottom material from true oceanic formations were found by various investigators to contain fewer bacteria; in some cases these organisms were entirely absent, at least as shown by the tests employed.

BACTERIA IN THE MARINE PLANKTON

In addition to the water and marine bottom, there is a third center of bacterial activities in the sea, namely, the plankton, especially the phytoplankton. Waksman and associates (16) have shown that while the water of one of the stations taken in the Gulf of Maine contained only 4 bacterial cells per 1 cubic centimeter of the surface layer of water, the zooplankton collected at the same station contained 890 bacteria per cubic centimeter of tow. A corresponding difference was found between the bacteria in the water and the diatom plankton in the water of George's Bank; on the average of two stations studied, the water contained 49 bacteria per 1 cubic centimeter and the plankton 37,000 cells in 1 cc. of tow. A study of the development of diatoms and bacteria in closed bottles carried out in coöperation with Professor Gran, brought out the fact that a definite parallelism existed between the development of the two groups of organisms; however, when the diatoms began to die off, the bacterial numbers still remained high.

In those investigations, where organic matter determinations were made, a definite parallelism was obtained between the abundance of bacteria and organic matter content; this points definitely to the fact that the most important controlling factor in the distribution of bacteria in the sea, both in the water and in the bottom, is the abundance and nature of the organic matter. Factors influencing the changes in the distribution of the organic matter will also influence changes in bacterial development.

MICROSCOPIC METHOD FOR STUDYING DISTRIBUTION OF BACTERIA IN THE SEA

The results of the investigations of the abundance of bacteria in the sea reported previously were all obtained by the use of the plate culture method. When the direct microscopic method was introduced, it was found that the actual numbers of bacteria in the sea (living and dead) are at least about a thousand times higher than the numbers obtained by the plate method, as shown by Cholodny (3), Butkewitch (2), and others. A somewhat narrower ratio, namely one of about 200:1, was obtained at the Woods Hole Laboratory, as shown by the following summary:

ABUNDANCE OF BACTERIA IN SEVERAL SAMPLES OF DIATOM TOW, AS SHOWN BY THE PLATE AND DIRECT MICROSCOPIC METHODS[1]

*Station No.**	*Nature of Tow*	*Numbers of bacteria in 1 cc. of tow*	
		Plate method	*Direct microscopic method*
1695	Surface tow	1,600,000	346,900,000
1697	Surface tow	3,500,000	202,400,000
1698	Deep tow	1,200,000	205,200,000
1699	Surface tow	600,000	234,000,000
1700	Surface tow	120,000	265,950,000
Average		1,404,000	250,890,000

These results are sufficient to emphasize the fact that the numbers of bacteria obtained by the plate method represent only a small fraction of the total bacterial population of the sea. This is due to several causes: 1. Many types of bacteria are unable to develop on the artificial medium, since no one medium can be devised which would be favorable for the growth of all bacteria; 2. Many of the bacteria in the sea, especially in the plankton and bottom material, occur not as individual cells, but as clumps which are not readily broken up in the preparation of the dilution for plating; 3. Many of the bacteria are dead, while others represent weakened cells which, for one reason or another, do not develop on the artificial media.

With all these limitations, however, the plate method offers a very convenient method for comparative studies of bacterial distribution in the sea; it should, however, whenever possible, be supplemented by the direct microscopic method.

NATURE OF BACTERIAL POPULATION IN THE SEA

As to the specific nature of the bacterial population of the sea water and the sea bottom, even a few general observations will bring out the fact that a marked difference exists between the two. In the case of the bacteria in the water, aerobic and non-spore forming organisms are found to predominate. In the bottom material, spore-forming and anaerobic bacteria are very abundant and may at times even predominate; these bacteria increase in

* Gulf of Maine or George's Bank.

[1] The microscopic counts were made by Dr. M. Hotchkiss, while in making the plate counts, the writer was assisted by Dr. C. Carey.

relative numbers with an increase in depth of the bottom material, especially in the case of mud bottoms.

The sea bottom represents a specific habitat for the development of such important groups of organisms as the nitrifying bacteria, the anaerobic nitrogen-fixing bacteria and the humus-decomposing organisms, although the available information concerning the last group is still very limited. On the other hand, the sea water, including the plankton, represents a more favorable habitat for the development of bacteria decomposing fresh organic matter, namely, the cellulose-decomposing, alginic acid decomposing, agar-liquefying, protein-decomposing and other groups of bacteria. The development of these specific bacteria in the sea will be directly correlated with the chemical nature of the plant and animal residues in the sea and their transformation products (18).

CONDITIONS RESPONSIBLE FOR BACTERIAL DISTRIBUTION IN THE SEA

Two conditions are primarily responsible for the development of bacteria in the sea:

1. The supply of available nutrients. In addition to the abundance of organic matter in the sea water and the sea bottom referred to above, one must also consider, (a) the nature of this organic matter, (b) the extent of its decomposition, (c) presence of mineral elements essential for microbial development, and (d) abundance of elements and compounds which can be used as direct sources of energy by certain specific bacteria, such as H_2S, S, H_2, NH_3, NO_2 and CH_4. It was shown (17), for example, that in the decomposition of *Fucus* in the sea by bacteria, there is a direct parallelism between the numbers of bacteria and extent of decomposition of the algal material. The addition of a small amount of available nitrogen which favored this decomposition also favored bacterial multiplication.

2. The environmental conditions. The importance of aeration, temperature, salinity and reaction upon bacterial development is well established. When a sample of water is brought into the laboratory and placed under favorable temperature conditions, rapid bacterial multiplication takes place (6); this tends to show that the particular water contains organic substances, either in solution or in suspension, which can be used as nutrients by the bacteria, as soon as temperature conditions are made favorable.

The distribution of bacteria in the sea is thus found to be controlled by a number of factors, which are of primary importance in the cycle of life in the sea. In their turn, the marine bacteria contribute an important share to the plant and animal life in the sea, through their activities in the processes of mineralization of organic residues, and in the transformation of various elements and compounds.

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FACTORS AFFECTING THE VERTICAL DISTRIBUTION OF COPEPODS

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For planktonic organisms the world is three dimensional; and for them the vertical dimension is perhaps the most important. The factors which bring about the vertical distribution of planktonic populations are therefore of considerable interest (*cf.* Russell, 1927). Let us investigate these factors in the environment of a copepod, since we have considerable information about this type of animal, and inquire as to the *modus operandi* of each. The principles involved are universal in their application and may be used in the interpretation of the vertical distribution of any planktonic community in any large body of water. Many apply to problems of horizontal distribution as well.

The depth at which a copepod finds itself is due in part to mechanical forces which transport it bodily through the water and in part to its own swimming activity. In response to gravity, the most important of the former, the population is continually tending to sink. Immature copepods, having larger areas for their masses, do not fall as rapidly as do the adults. For a given individual the rate of sinking depends upon the viscosity of the water which in turn is affected by the temperature and pressure. Under laboratory conditions large copepods have been observed to sink at rates of about 40 cm./min. (*cf.* Parker, 1902; Gardiner, 1933). The action of gravity is therefore a serious matter for these forms. In regions where upwelling exists on a large scale, the animals may be carried toward the surface by the current faster than they tend to sink through the water. In most parts of the sea, however, vertical movements of water masses are of limited extent and often take place in a downward as well as an upward direction.

Turbulence due to wave action is continually causing suspended objects to be dispersed throughout the water mass. Plankton concentrated near the surface will tend to be carried downwards, and populations in deep layers will tend to be transported toward the surface by the vertical component of this force. Now the coefficient of turbulent conductivity is greatest at the surface and diminishes with depth. This means that for organisms inhabiting an intermediate zone, upward scattering will take place faster than downward scattering. For the vertical distribution of the phytoplankton turbulence is obviously of great importance. But this factor is ordinarily of negligible effect for such strong swimmers as copepods according to calculations kindly furnished by Prof. C. G. Rossby. In the Gulf of Maine, for example, it is

[1] Contribution No. 41.

only during the winter storms that turbulent conductivity is sufficiently strong to have an appreciable influence upon the distribution of the copepod population to any considerable depth, and in the summer its effect would be felt only in the surface stratum during the severest storms.

Besides translocational influences of this sort the relative distribution of the population may be affected by the actual addition or removal of individuals at particular depths. Rapid reproduction within a limited zone is a case in point, and although the affect would probably not be appreciable in a copepod community, it undoubtedly is important for the phytoplankton. The distribution would be modified in the reverse manner by the consumption of individuals at certain depths by other organisms or by death resulting from movement into strata where lethal conditions exist.

Copepods are rapid swimmers for their size. From laboratory experiments we know that copepods can swim in a horizontal direction as fast as 136 cm./min. (Welsh, 1933). Such animals would theoretically be able to swim upwards at this rate less the sinking rate, or approximately 100 cm./min. If such a speed can be maintained over any considerable period of time, it would appear that the vertical distribution of copepods is chiefly determined by the swimming activity of the animals themselves. We must, therefore, proceed to inquire to what extent the hydrographic and biological features of the environment are important in controlling the direction and the speed of movement of the copepods.

It is essential to establish the fact at the outset that an organism cannot respond in a directional manner to any environmental agent unless the difference in the stimulation of two parts of its body is discernible. This means that the intensity of the agent in one direction must be perceptibly greater than in another direction. For example, in large bodies of water, the change of temperature with depth is certainly too gradual for any organism as small as a copepod to perceive in which direction it is becoming greater or in which direction becoming less. The most rapid change of temperature with depth observed during observations on copepods in the Gulf of Maine was a change of 1 degree in 1.5 meters (see Figs. 1 and 3). Even for this extreme case the difference in temperature at the two ends of an organism 5 mm. long would be only 0.003°C. Temperature may, and often does, affect vertical distribution indirectly, as is described below, but it cannot of itself orient the swimming movement of the organism.

The ever-present force of gravity may be listed as of prime importance in regulating the swimming of copepods. Gravity exerts its pull from one direction and the copepods are oriented in the vertical plane accordingly. The animals may also respond positively or negatively to this directional force by geotropic swimming movements. Whether the geotropism will be positive or negative depends upon physiological regulation by internal and external factors.

Light is a second agent which may have a directional effect on the movement of the copepod. This factor can operate only during the daytime and near the surface where the direction of propagation of the light is perceptible. This condition may obtain to considerable depths since Poole and Atkins (1929) found that even at 25 m. the vertical light is twice as great as the horizonal light. The sign of phototropic swimming is determined by the intensity of light and by other factors such as temperature. At depths where

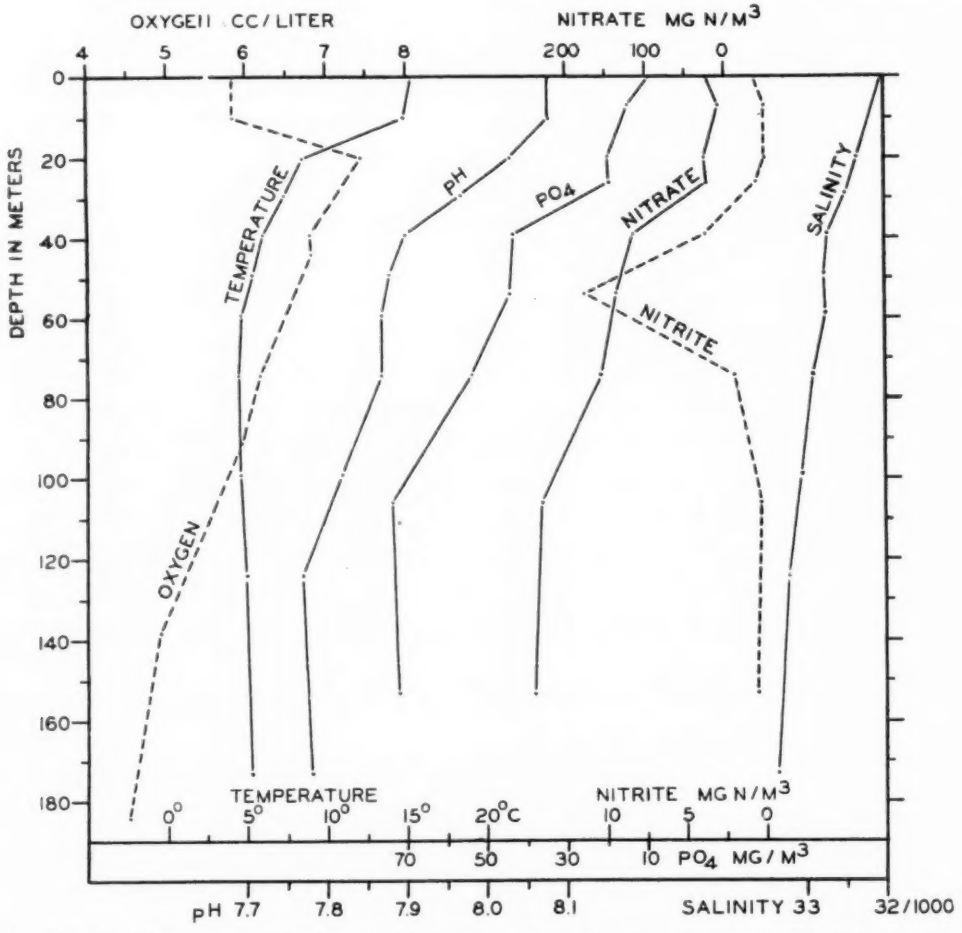

FIG. 1. Variation of hydrographic factors with depth. Station 1287, July 10-12, 1932, Lat. 43°04′ N. Long. 69°24′ W. (except for oxygen which is for Station 1285, July 9, 1932, Lat. 42°34′ N. Long. 69°37′ W.)

the illumination is completely diffuse, phototropic responses can no longer take place. The intensity of the light present may, however, affect the sign of geotropism.

Temperature, as already pointed out, changes so gradually with depth (see Fig. 1) that the difference in amount of heat reaching a copepod from any two directions is imperceptible. Under these circumstances no thermotropism can exist. Temperature can, however, affect the sign of geotrop-

ism and phototropism. Secondary affects of this sort have been demonstrated repeatedly in the laboratory (*cf.* Rose, 1929). Accordingly, temperature may play a very important rôle in controlling the vertical distribution of plankton, but its action is indirect and it can affect only those animals which exhibit geotropism or phototropism.

The vertical gradients of the salinity, the pH, the concentrations of oxygen and other substances which are widely distributed through the water are again almost certainly too gradual for the organism to perceive the change (see Fig. 1). Even if the copepod possess sense organs specialized for the detection of these substances, orientation cannot be brought about if the difference in the stimulation of two parts of the body is not above the threshold of discrimination for the organism. It is impossible for the copepod to "tell" in which direction salinity, for example, is increasing, and in which decreasing. If such features of the environment do affect the vertical movements of copepods at all, they can do so only by modifying geotropism or phototropism.

The presence of other organisms may influence the distribution of copepods. The direction in which actual contacts occur can, of course, be perceived and a copepod may even be able to tell whence came a vibration or a motion of the water. Avoiding reactions are responsible in part for the dispersion of the animals; processes of the reverse sort bring the animals together in swarms. During the breeding season male copepods have been observed in the laboratory to turn quickly and attempt to grasp other individuals which chanced to brush past them. Copepods undoubtedly do react in a directional manner to dissolved substances of a characteristic sort emanating from a highly concentrated source. A true chemotropism of this sort probably exists in the neighborhood of a relatively large decaying organism or in the wake of an individual of the opposite sex. The concentration gradient would be steep and hence perceptible in such cases as distinguished from those mentioned in the preceding paragraph.

Vertical movements in relation to a food supply have been suggested as important in the distribution of copepods (Worthington, 1931). We have evidence that copepods do not pick out discrete particles in feeding, but filter everything in their path (Cannon, 1928). If this is true, can they direct their swimming movements into regions where food is abundant? Here again the question of gradient and discrimination threshold is encountered. The change in concentration of phytoplankton organisms even at the limits of a zone of "abundance" is extremely gradual in comparison with the size of a copepod. Under these circumstances it is difficult to believe that a copepod could perceive in which direction food organisms are increasing in abundance and in which direction they are decreasing. This reasoning would apply to stimulation received both from actual contact and from diffusing chemical

substances. If the organism fed by swimming after separate particles of food, then it would be automatically carried toward zones of greater concentration by the laws of chance. For continuous filter feeders under conditions varying too gradually to be perceived, it seems necessary to conclude either that only those animals survive which happen to swim in the right direction, or that the absence of food in the digestive tract influences geotropism or phototropism suitably to bring the animals to levels where edible organisms are ordinarily found.

There are, then, only two or possibly three ways in which a copepod may tell "which way is up": orientation may be brought about by gravity, by light, or possibly by stimuli received from other individuals. However, it is not the direction of movement alone which determines the configuration of the copepod population; the speed and duration of swimming also contribute to the results. We know from many laboratory observations that the light intensity and the temperature of the medium influences profoundly the rate of movement of planktonic animals. The concentration of dissolved substances may operate in a similar fashion under certain circumstances.

When tested in the laboratory an increase in illumination or in temperature ordinarily causes an acceleration of the swimming rate, and a decrease in either results in retardation. But these characteristic effects on swimming speed appear to operate in the wrong direction for the usual situation in nature. Consider a copepod inhabiting a certain stratum of water. In the typical case the animal would appear to be confined to this range because the light intensity or the temperature is too high above the upper limit and too low below the lower limit. Now the animal must always be swimming upwards to some extent to compensate for its tendency to sink. If our laboratory observations are correct, we should expect the copepod to increase its rate of swimming when it rose into brighter and warmer water layers. This would tend to carry it still higher in the water. Conversely, whenever the animal dropped into deeper water layers where temperature and illumination are reduced, we should expect, on the same basis, that its swimming activity would diminish and that the animal would consequently sink to greater and greater depths. Undoubtedly many animals on the outskirts of the population are continually being killed off as they are carried farther and farther from tolerable conditions in response to these reactions. At the upper limit of the range the increasingly lethal conditions would probably cause paralysis before becoming actually fatal. The organism would consequently sink and if it reached favorable conditions soon enough, might thus escape death in this case. However, this mechanism would just make matters worse at the lower limit of the range: paralysis would result in even faster sinking away from the habitable zone. But copepod populations do succeed in maintaining themselves above certain definite limits. The conclusion seems

unavoidable, in this case at least, that the decrease in illumination or in temperature, although it retards swimming, also reverses the sign of geotropism (or of phototropism) with the result that the copepod is stimulated to swim upwards.

Finally the duration of the copepod's swimming movement is in part responsible for the actual distribution which we observe at any given moment. A study of the seasonal changes in vertical distribution is not concerned with this third factor because there is plenty of time for an equilibrium to be reached. However, in an investigation of the depth of the copepod population at different hours of the day, the duration of the movement is decidedly important. There may not be time enough for equilibrium to be reached before a change in environmental conditions produces new reactions in the animals. This whole question is obviously bound up with the problem of diurnal migration which has been extensively studied in recent years (Russell, 1931; Worthington, 1931; Southern and Gardiner, 1932; Nicholls, 1933; Clarke, 1933, 1934). A specific example of diurnal migration will illustrate this point and also reveal the application of the questions discussed above to a practical problem.

Figure 2 shows diagrammatically the diurnal migration of the adult females of *Metridia lucens* during July 10, 11, and 12, 1932 at a station in the Gulf of Maine (Clarke, 1933). The lines of equal light intensity (1000 μW/cm^2, 100 μW/cm^2, etc.) drawn in the figure indicate the changes in submarine irradiation to which the copepods were subjected during the course of each day. Inspection of the diagram reveals the fact that in general the zone of maximum abundance of *Metridia* occurs between the light intensities of 10 μW/cm^2 and 1 μW/cm^2 (or less) and rises and falls coincidently. Early in the morning and late in the evening the light intensity changes very rapidly, and we might expect that the animal could not "keep up" with its zone of optimum illumination. For example, it can be roughly calculated from the figure that the position of the 1-microwatt line rises about 46 meters in the hour between 19 and 20 o'clock. To keep pace with this a copepod would have to swim vertically upwards at an average speed of 77 cm/min. Such a speed would actually be possible according to the calculations made earlier. But for populations living at greater depths during the daytime and exhibiting a positive phototropism during the afternoon, the intensity of light reaching them may well become imperceptibly weak before the animals ever reach the surface strata. However, geotropism frequently is in operation also, as in this case of *Metridia*, since the copepods continued to swim toward the surface after complete darkness.

Light is obviously the chief factor which changes during each daily period but other factors which may affect vertical distribution directly or indirectly should be examined for diurnal fluctuations. Hydrographic measurements

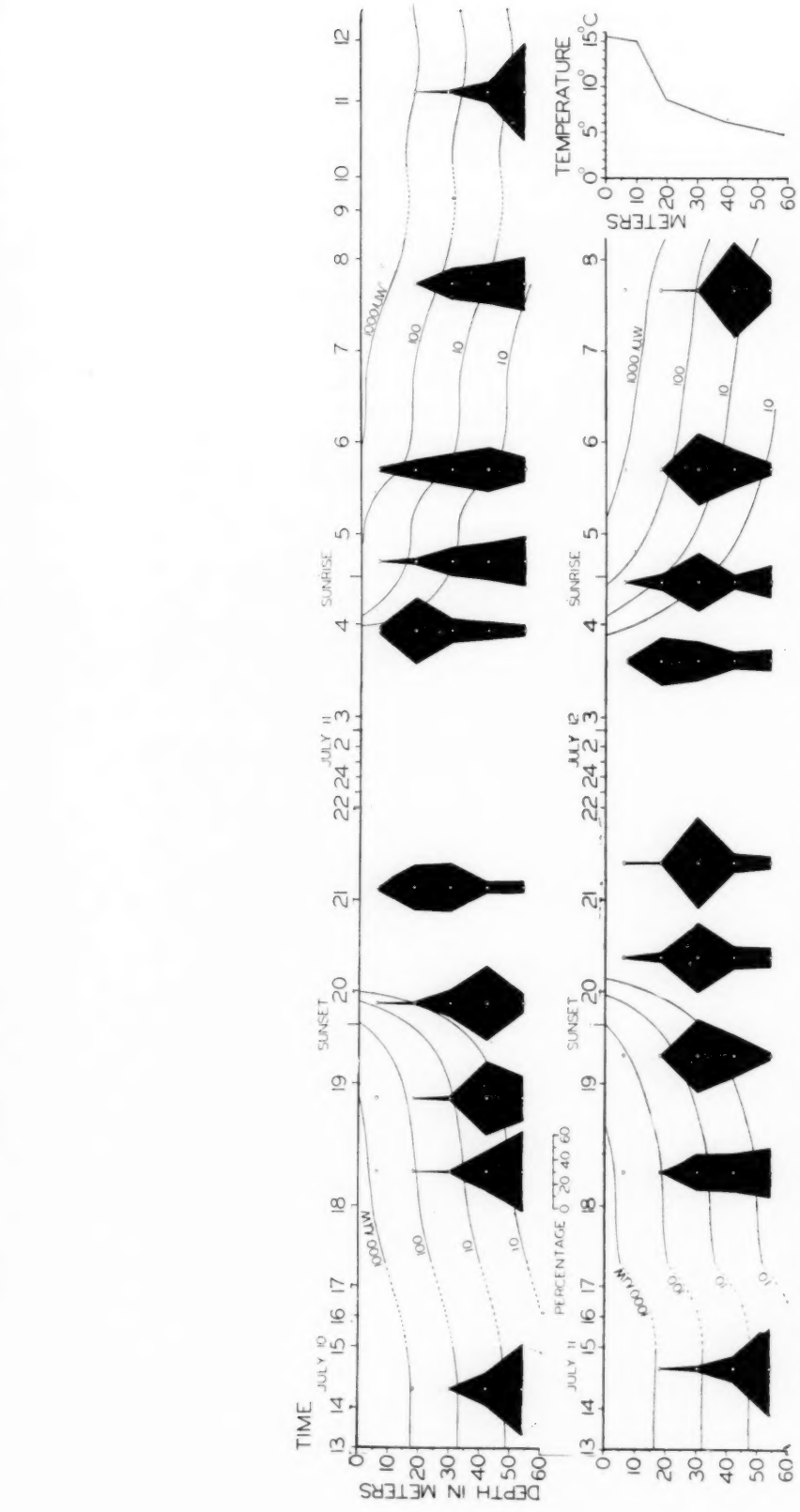

FIG. 2. The diurnal migration of the adult females of *Metridia lucens* during the 48-hour period of Station 1287 (July 10-12, 1932, Lat. 43°04′ N. Long. 69°24′ W. The changes in the light intensity are indicated by the lines representing the depth at which 1000 μW/cm^2, 100μW/cm^2, etc., occurred. (One microwatt/cm^2 may be taken as approximately equal to 3 meter-candles as used by Poole and Atkins, 1929). Where the lines are broken, a shortening of the time scale is indicated merely; observations were not discontinued during these periods. The temperature curve for this station is reproduced in the lower right-hand corner.

made within a day or two of these observations on *Metridia* showed that no significant diurnal changes in the hydrogenion concentration, in the oxygen content, or in the temperature were taking place in this region. Variations in the depth of food organisms during such short periods are likewise highly unlikely. However, a year later at another station in the Gulf of Maine more complete measurements of the temperature told quite a different story. The results are shown in Fig. 3. Measurements of temperatures were made every five meters to a depth of fifty meters and the series was repeated 19 times during the 54-hour period. The isotherms show two sharp peaks: one at 5 o'clock, July 15, and the other at 6 o'clock, July 16. There are three less prominent peaks alternating with these, the whole series showing a very decided tidal rhythm. The phenomenon is obviously controlled by the tides but the complete explanation is not known.

We are accustomed to think of temperature changes in the sea as being very gradual. Such diurnal changes as are known to occur are ordinarily due to heating by the sun. This effect can be seen in the present case in the variation of the temperature at 1 meter. The difference between the highest and the lowest temperatures at this depth was only 0.9°C. But at a depth of 28 meters the temperature changed from 7°C. to 12°C. between 5 and 8 o'clock of July 15. In this extreme case there was a variation of 5° in three hours! If temperature changes of this magnitude occur generally in the Gulf of Maine or elsewhere, the vertical distribution of plankton must be profoundly affected. Hydrographers, too, must reckon with such diurnal fluctuations.

It would be impossible, of course, for a body of water actually to change

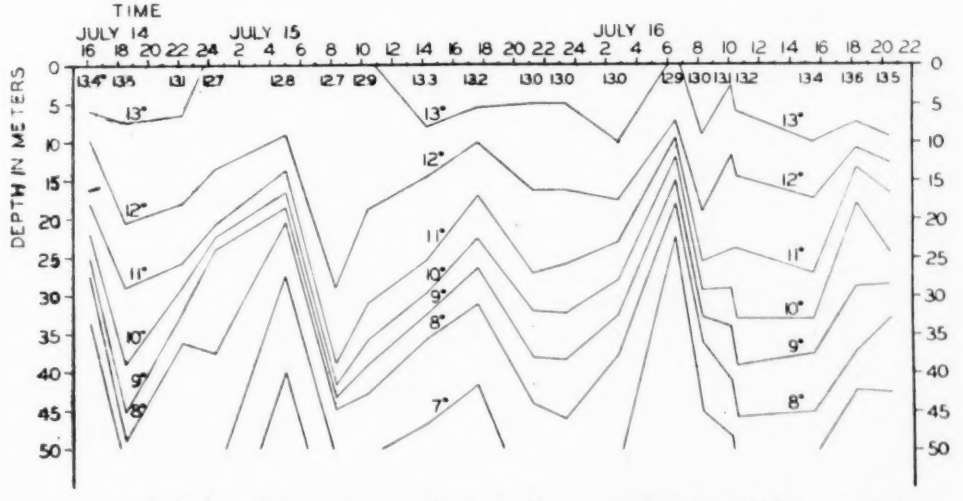

FIG. 3. Variation of temperatures down to 50 meters during a 54-hour period.

Station 1722, July 14-16, 1933, Lat. 42°50′ N. Long. 67°05′ W. Nineteen series of measurements were made at the hours indicated (24-hr. scale). The temperatures at the top are for the 1 meter level. The black dots indicate the half-degree points.

its temperature to such an extent under these circumstances. The effect must have been produced by a vertical movement of whole strata of water. For example, the position of the thermocline is seen to have been displaced downwards 25 meters during the 3 hours following 5 o'clock, July 15. Now the plankton would tend to be carried bodily up and down with the masses of water in which they are suspended. The question at once arises whether active forms like the copepods could maintain their positions in depth by swimming in the appropriate direction. This would be possible since the maximum rate of water movement is only about 14 cm/min. If they did so, they would experience wide changes in the temperature of their surroundings.

Observations on the diurnal migration of *Calanus finmarchicus* at this station (Clarke, 1934) reveal a vertical movement of the population from depths as great as 138 m. during the day to the 6 meter level at night. These animals were "on the go" continuously except during the middle of the day and the middle of the night. At these periods the population was respectively below and above the zone of extreme temperature change. But at dawn and at dusk *Calanus* carried out its migration right through the thermocline. The responses of this animal to gravity and to light are therefore stronger than those to temperature.

In conclusion let us review our findings in regard to the action of all these environmental factors upon the copepods. Of the mechanical forces, sinking due to gravity is the only one of serious importance. Gravity can be overcome by swimming, and, in the last analysis, the vertical distribution of copepods is determined by their own swimming activity. Directional movement can be caused only by gravity, light, and possibly the presence of other organisms, but other factors may have an indirect effect through modification of whatever geotropic or phototropic reactions are in operation. The speed and duration of the swimming also play their parts in controlling distribution. Speed is modified ordinarily by illumination and temperature. The time available for swimming depends upon the rate at which the environment becomes altered. Light changes more rapidly than any other factor; but temperature, in one case at least, is shown to fluctuate profoundly. Even in respect to these factors copepods can adjust their distribution with the necessary speed through their own swimming activity.

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NOTE

During the discussion which followed the presentation of this paper at the meeting of the Ecological Society of America on December 30, 1933, Dr. V. E. Shelford called my attention to certain experiments on the responses of animals to gradients performed by him and his associates.[1] In these experiments it appears that the animal "turns back from a weaker stimulus after encountering a stronger one; the threshold of stimulation is lowered." It is possible that the sensitivity of an animal in nature may be similarly increased. However, a limit must eventually be reached,—that is, a situation where the gradient of such a factor as temperature is so low that the animal, in its most sensitive condition cannot "perceive" in which direction the intensity is increasing and in which decreasing. Another sort of increase of sensitivity would result from rapid swimming in a direction perpendicular to the gradient thus augmenting the rate of intensity change in time. This might result in an "avoiding reaction" which would not otherwise have been produced. Here again a limit is reached when the gradient is so low that no response is evoked at the maximum swimming speed. Even if copepods possess some sort of "memory," this would be of no service for orientation when in a uniform environment, such as the open ocean, any more than it is for a man lost in a fog. There is, then, a definite limiting threshold gradient below which the organism cannot respond directionally. Obviously the precise value of the threshold gradient for copepods can be found only by

[1] Shelford, V. E., A comparison of the responses of animals in gradients of environmental factors with particular reference to the method of reaction of representatives of the various groups from protozoa to mammals. *Science*, N. S., 48: 225-230, 1918.

direct experiment. However, the evidence presented in the foregoing paper indicates that in the ocean the gradients of such factors as temperature are below the threshold for copepods. It does not appear that the experiments of Shelford and his associates nor those of any other investigators with which I am familiar cast doubt upon these conclusions.

CONCERNING THE ORGANIZATION OF MARINE COASTAL COMMUNITIES

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One of the more intelligent of our university presidents once said that Ecology seemed to be the study of the sty with the pig left out. Modern studies of oceanography have seemed to me to deserve, at times, the same definition. The oceanic sty is so complicated and vast and beautiful that it is not to be wondered that it attracts attention as compared with the less obvious oceanic pig. Fortunately, the emphasis given in the present symposium shows that the latter is not being entirely neglected even though as yet, no one seems able to see the whole pig. If as a result of my remarks you are tempted to think that I have my attention fixed so low as to be able to see the pig's feet only, I assure you that the defect is more apparent than real, and is caused by the greater ease of focusing on the littoral animal communities of the bottom, than upon those of the entire waters.

When we examine the work of ecologists we find that Ecology has, among other services, kept alive and focused naturalistic interests; it has prevented physiology from becoming entirely immersed in laboratory analyses, and has insisted that populations exist in nature as well as in *Drosophila* culture bottles or human mortality tables. However most of us agree that the distinctive contribution of ecology to the biological complex has been the emphasis on the fact that organisms live in communities. A brief survey of the development of the concept of communities and consideration of their properties will help us to evaluate their importance in oceanography and perhaps throw some light upon the problems now awaiting solution in marine ecology.

The recognition of the existence of communities of living organisms in nature is not as new as many appear to think. Philosophically the idea dates back to the classical Greeks. In the modern period, according to Braun-Blanquet (1932), Heer (1835), Lecoq (1854), Sendtner (1854) and Kerner (1863) all sought to understand the basic causes of the social relations of certain plants, and Kerner "brought even to the laymen an understanding of the relation of the principal plant communities of Austro-Hungary to the environment." Darwin, in "The Origin of Species" showed a clear understanding of the web-of-life conception of community organization, as witness his famous demonstration of the relationship between the number of cats and the amount of clover seed in an English community. St. Hilaire (1859) foreshadowed, and Haeckel (1869) in his classical definition of "Oecology" also vaguely recognized the existence of communities.

As Dr. Vaughn has already said, E. Forbes in 1843 in his study of the distribution of molluscs and radiates of the Aegean Sea found "provinces of depth" which "are distinguished from each other by the associations of the species they severally include. Certain species in each are found in no other; several are found in one region which do not range into the next above, whilst they extend to that below, or *vice versa*. Certain species have their maximum of development in each zone, being most prolific in individuals in that zone which is their maximum, and of which they may be regarded as especially characteristic. Mingled with the true natives of every zone are stragglers, owing their presence to the secondary influences which modify distribution."

The subdivision of littoral regions into faunal provinces, as Dana (1852, 1853), Packard (1863) and Verrill (1866) have done for Atlantic coastal waters, is based primarily on the observed distribution of species and groups of species and secondarily on physical factors such as temperature and geographic features such as capes. The Floridian, Carolinian, Virginian, Acadian and Syrtensian faunas of these naturalists suggest the biomes (biotic formations) of modern workers (cf. Shelford, 1930). If proposed today they would be designated by biological terms suggesting their taxonomic composition, rather than by geographic terms which suggest their distribution.

We now know this to have been the historical background against which we should view the remarkable work of Verrill (1874) upon "The Invertebrate Animals of Vineyard Sound and Adjacent Waters," which despite the praise given by Adams (1913) has not received the recognition nor had the influence among ecologists which it merits. In this work Verrill undertook, among other projects, "the exploration of the shores and shallow waters for the purpose of making collections of all the marine animals and algae living between tides, on every kind of shore . . . and to ascertain as much as possible concerning their habits, relative abundance, stations, etc." He was also concerned to extend these studies to the deeper waters with the aid of such apparatus as was available.

He soon found there were "three distinct assemblages of animal life which are dependent upon and limited by definite physical conditions of the waters which they inhabit." These primary groups were:

1. The fauna of the bays and sounds.
2. The fauna of the estuaries and other brackish waters.
3. The fauna of the cold waters of the ocean shores and outer banks and channels.

In each of these assemblages Verrill recognized that certain kinds of animals are restricted to particular localities, depending on the character of the bottom or the shore. "Thus," he says, "there will be found species or even groups of species which inhabit only sandy shores, others which dwell

in the muddy places; and still others that prefer the clean gravelly bottoms where the water is several fathoms deep." These and other subdivisions are shown to exist within the larger assemblages. For example, under the general heading of "animals of bays and sounds" he set up the following subdivisions of the general habitat.

1. Rocky shores between the tide lines.
2. Sandy and gravelly shores.
3. Muddy shores and flats.
4. Piles of wharves; buoys, etc.
5. Rocky bottoms below the low water mark.
6. Stony, gravelly and shelly bottoms, do.
7. Sandy bottoms, do.
8. Muddy bottoms, do.
9. Free-swimming and surface animals.
10. Parasites.

These may be further subdivided; thus, for example, regarding the animals living in the mud he says: "The character of the mud itself is quite various and the different kinds are often inhabited by different groups of animals." The following were recognized by Verrill:

1. Thick heavy clay containing few species.
2. Fine sand and clay, more favorable to animal life.
3. Soft flocculent mud containing quantities of microscopic plants and animals; an extremely favorable habitat for many bivalves, annelids, the local holothurians and many fishes.
4. If "3" is underlaid by sand or gravel a few inches below the surface, oyster beds may develop with their associated organisms.

Few animals, Verrill says, are strictly confined to one of these subdivisions, and the majority are found in two, three or more of them and often in equal abundance, "though each species generally prefers one particular kind of locality." He knew that the day population differed from that found at night in the same spot and that there were seasonal changes, but concluded that "the more common and characteristic species are, however, pretty constant in their habits and may be easily found in their respective stations at almost any time."

In describing the animals belonging to these different habitat divisions and subdivisions he reports, "It has not been found desirable to mention in this part of the report (the general discussion) all the species found in each, but only those that appear to be most abundant and important." These, I take it, are what would now be termed by current investigators the dominant, characteristic, or prevalent species.

This somewhat extended review of Verrill's work indicates correctly that he was impressed with the organization of communities upon the basis of

their relations with their physical habitat rather than as a result of their interrelations with each other. The latter were not unknown to him, for he states that *Molgula manhattensis* is generally associated with *Styela (= Cynthia) partita*. Often the abundant *Perophora viridis* covers these, as well as other ascidians, algae, hydroids, etc. In another place he states that this same group of species live together on wharf pilings, and adds that *Amaroucium constellatum* is "associated" with them.

Again he says, "Shells of oysters provide suitable attachment for various shells, bryozoans, ascidians, hydroids, sponges, etc., which could not otherwise maintain their existence on muddy bottoms, while other kinds of animals such as crabs, annelids, etc., find shelter between the shells or in their interstices." Thus Verrill saw certain of the interrelationships that exist in an oyster bank. A few years later Möbius (1877) wrote of these in greater detail with a thoroughly modern understanding of their implications, as is shown by the following quotation:

"Every oyster-bed is, to a certain degree, a community of living beings, a collection of species, and a massing of individuals, which find here everything necessary for their growth and continuance, such as suitable soil, sufficient food, the requisite percentage of salt, and a temperature favorable for their development. Each species which lives here is represented by the greatest number of individuals which can grow to maturity under the conditions which surround them. . . . Science possesses as yet no word by which such a community of living beings may be designated; no word for a community where the sum of species and individuals being mutually limited and selected under the average external conditions of life, have, by means of transmission, continued in possession of a certain definite territory. I propose the word *Biococnosis* for such a community. Any change in any of the relative factors of a biocönose *(sic)* produces changes in other factors of the same. If, at any time, one of the external conditions of life should deviate for a long time from its ordinary mean, the entire biocönose or community would be transformed. It would also be transformed if the number of individuals of a particular species increased or diminished through the instrumentality of man, or if one species entirely disappeared from, or a new species entered into, the community."

The same conception was worked out more fully by S. A. Forbes (1887) in his recently much quoted essay on "The Lake as a Microcosm." Essentially the same conclusions were reached by Warming (1895) in his study of the vegetation of the Danish dunes. According to Braun-Blanquet, who follows the usual custom of disregarding the zoölogical studies we have just reviewed, Warming's work is the most important landmark in the development of synecology since Heer. The social nature of plant communities was recognized by Warming, who also saw that they form superorganismal units.

Braun-Blanquet's estimate of the importance of Warming's contribution is just, in that modern community studies have been stimulated largely by his work rather than by that of his predecessors, E. Forbes, Verrill, Möbius, and S. A. Forbes.

From the impetus given by Warming came the rapid development of the science of plant communities, which has progressed sufficiently until today we have a fair outline of the problems involved and methods of procedure in matters pertaining to the composition, organization and distribution of such communities, and know many of the basic facts as well. Workers have been busy for the last thirty years picking up the advances made in knowledge of the organization and other relations of plant communities and applying them to animal communities. The important recent advance, which emphasizes the unity of the biotic community, is a case in point, originating in its modern form apparently with a statement by Clements;[1] its support, as shown by Phillips (1932) has come largely from the zoölogists (cf. Shelford, 1932). Like that of Verrill, much of the early work on animal communities after Warming's time was organized about the environment (cf. Shelford, 1913), a condition which holds in many quarters even today (cf. Elton, 1933); there is added, however, the dynamic concept of community evolution usually called succession, which was also taken over from the botanists.

The introduction of quantitative methods came early; again the botanists took the initiative (Pound and Clements, 1898, Clements, 1905). In 1907 Forbes, studying the distribution of Illinois fishes, applied statistical methods to collection data to determine frequency of association of species. He was concerned not with the problem of the total population of the fishes but with the number of times associated fishes were collected together, as compared with the number of times each was taken separately. The quantitative urge must have been pretty generally in the air. Shelford (1911) made a quantitative estimate of the physical and biotic factors associated with succession of pond fishes. Working under Shelford's influence I wrote (Allee, 1911): "Qualitative work, however, is not sufficient ground on which to base exact conclusions (concerning seasonal succession). It is also necessary to have exact data regarding the abundance of each of these species (of pond animals) throughout the year." This statement is read into the record to show that Dr. Shelford and I were alive to the needs of the time.

The quantitative work which has had an influence, particularly in marine ecology, is that of Petersen and his associates. In 1911 Petersen and Jensen reported the first of a series of quantitative studies of animal life on the sea bottom near Denmark. Using his now well-known bottom sampler, Petersen and his co-workers set out to study the life of the sea bottom in its relation to fish food. They soon discovered, after quantitative methods were employed,

[1] Dr. Clements informs me in a personal communication that he used the term "biome" in its present connotation at the Columbus meetings of the A. A. A. S. in 1915.

that these bottom dwellers live in recognizable communities which can be satisfactorily designated by one or more of the "predominant" species, and without listing all the members of the community (cf. Verrill, p. 543.) These predominant species were determined by considering the abundance and weight of non-seasonal animals taken in different bottom samples from known areas; "their consideration gives a good idea of the outer conditions on which the community is dependent."

The biocoenose-like communities, while usually correlated with a definite environment, are regarded as entities in themselves rather than as mere appendages of a particular physical habitat. Petersen focuses on the "pig" of our original metaphor and leaves the "sty" in the background. Although the communities change with decided difference in substratum and depth and salinity, none of these are all important.

A series for the level bottom founded in part on habitat characters, is recognized by Petersen (1918) as follows:

1. *Macoma* community, all along the shallow water of the coasts; 0.3 M. at high tide, dry at low water; in Baltic to 40-50 M.
2. *Abra* community often with *Echinocardium;* especially in the Belt Sea and the fjords, 16-18 M.
3. *Venus* community with *Echinocardium;* open sandy coasts of the Kattegat and in the North Sea, 10-11 M.
4. *Echinocardium-Filiformis* community, at intermediate depths in the Kattegat, 20-22 M., soft clay and sand.
5. *Brissopsis-Chiajei* community, in deepest parts of the Kattegat, 60-75 M., soft clay.
6. *Brissopsis-Sarsii* community, deeper parts of the Skagerack, 186 M., soft clay.
7. *Amphilepsis-Pecten* community, deepest parts of the Skagerack, 320-328 M., soft clay.
8. *Haploops* community, locally in southeastern Kattegat, 27 M., soft clay.
9. The deep *Venus* community, sporadically in the Kattegat, sand.

The *Macoma* community with its chief and characteristic animal, *Macoma baltica*, and its many facies, which depend on type of bottom and plant growth, can live far up in the brackish Baltic water with a salinity of about 6 per mille and less (Petersen, 1913). They are eurythermous and euryhaline animals. Even so, they are lacking in almost the whole of the Kattegat where a number of other salt water animals occur. Judging from their habitat tolerances, they should be found in the *Venus* stations, but in fact are found only where the "*Venus* community" is lacking. *Mytilus* of the *Macoma* group lives on buoys in the *Venus* territory of the Kattegat, but of course the constituents that are limited to the bottom cannot be found there. It must be, Petersen says, that *Echinocardium* and *Ophioglypha* and the plaice fishes exclude them. These are lacking where the *Macoma* animals occur and form their boundary on the deep water side. "*Venus* animals" cannot reach up on the buoys in

the Kattegat and destroy the *Mytilus* fry. Petersen found the distribution of the *Macoma* community understandable only by taking into consideration the biological factors which bring about competition with the "*Venus* community."

Amphiura eat young molluscs, and few or no molluscs are to be found when this echinoderm is present in numbers, although in neighboring inshore waters and in deeper waters where there are no *Amphiura*, molluscs are plentiful. The gammarid, *Haploops tubicola*, where "predominant" transforms the whole character of the bottom by its mud tubes. This, Petersen thought, is probably the reason why the *Brissopsis* community does not reach its normal development in the presence of *Haploops*. *Modiola modiolus* under favorable circumstances may be present in such numbers as to cover everything else and even fill the whole bottom with a layer of living molluscs. The Arctic species *Astarte borealis* and *Macoma calcarea* occur in the Belt Sea and in the Baltic in large numbers, but not in the northern Kattegat or in the North Sea, and only at widely scattered points, if at all, along the Norwegian coasts. They are relict species and require deep, cool water, low salinity and most important of all, absence of enemies.

The voracious echinoderms have important effects upon fish fry. The more successful of their fish associates have behavior or developmental devices which protect the young fishes. The effectiveness of the echinoderms in controlling the bottom is shown by the fact that the plaice larvae develop in deep dark water in the Baltic, where echinoderms are absent; but in the North Sea of the Kattegat they develop only near the beach in shallow water, because there, only, are there no echinoderms. Truly, as Petersen insisted, in studying the organization of the sea, we must consider biological as well as physical factors. Also as he has emphasized repeatedly, many of these biological relations are not revealed by quantitative studies alone, illuminating as these can be. Their elucidation requires information of the sort furnished by what is commonly called, and at times disdainfully dismissed, as naturalistic observations.

In the waters about Woods Hole, where Verrill worked and where my own marine experience was largely gained (Allee, 1919, 1923, 1923a, 1923b), the physical factors of the habitat appear to be the obvious and controlling agents in delimiting ecological communities. Tidal zones are relatively narrow, especially so in Vineyard Sound, and the inshore communities are much subdivided by physiographic forces. There, as it seemed to me ten years ago, the communities could best be named by their most outstanding feature or features, whether of physical habitat or of plant or animal component. The names actually given to the different communities reflects the general dominance of the physical habitat. The communities then recognized include those of the eroding shores as follows: Those of the open waters, of the

wharf pilings, of the exposed rocks and of the protected rocks. The latter may be called the rockweed community. The last three have intertidal and adtidal facies. The communities of the depositing shores include those of the sand bars, of the muddy sand (*Phascolosoma* communities) of the eel grass and muck (*Cumingia* communities and *Scoloplos acutus*[2] communities), of the marginal muck (*Thyone* communities) and the intertidal communities.

Each of these communities could be distinguished by physical habitat features but, at least to the experienced worker, the animal or plant names as used are a distinct aid in clarity of definition and, at times, in brevity as well.

In the Woods Hole waters, in regions where habitat features become relatively uniform over a considerable area, the animal communities are not necessarily uniform. The veteran Woods Hole naturalist, Mr. George M. Gray, in a personal letter has given his experience on this point:

"Do animals congregate or assemble in groups in certain spots or localities in preference to other places which appear to be equally good? Yes, I think this is true in many instances. I will first consider our dredgings of two years ago in Buzzards Bay. This Bay has a bottom which is mostly a dark bluish mud, sticky and tenacious and hard to run through sieves. Much of the Bay runs eight fathoms deep. There are isolated spots where there are rocks and gravel and the depth may vary. But most of our dredgings were made in the characteristic mud. We made between 35 and 40 hauls or stations in the Bay, as stated above mostly in mud. While in nearly all mud stations there were scattered *Nephthys incisa* there were other stations in which these worms were abundant. A few stations had *Pandora trilineata* in plentiful numbers, other stations had few or none. The same is true for *Eupleura caudata, Cithera convexa, Mactra lateralis* and other forms. There was no apparent reason why they should not be equally plentiful in all these stations which have the same sort of bottom. . . . In a few stations we found *Trophonia*, and in a very few stations, a peculiar *Balanoglossus* (?) or anterior ends of it. Now as far as we know the bottom of this Bay, especially the lower end, has been mud for years and years, and why should there be only spots where certain forms are abundant and equally good spots, to our judgment, where these same forms are scarce or absent?"

Even within the more narrow, restricted habitats the same differential distribution can be seen. Thus on the flats with short eel grass near North Falmouth, I have collected the brittle starfish *Ophioderma brevispina* for hours at a time, using a garden rake to pull them out of the eel grass. I have never seen them in summer in nature when they were aggregated, but when

[2] Peterson shrewdly chose echinoderms and molluscs to designate his communities, since these are readily identified even in the field and are easily preserved. Annelids, he says, are equally characteristic, but lack the technical advantages just given. From the report of Dawson (1931) I appear to have been mistaken with regard to the identification or distribution of the worm I called *Scoloplos acutus* and, pending further investigation, that worm cannot be regarded as a community index.

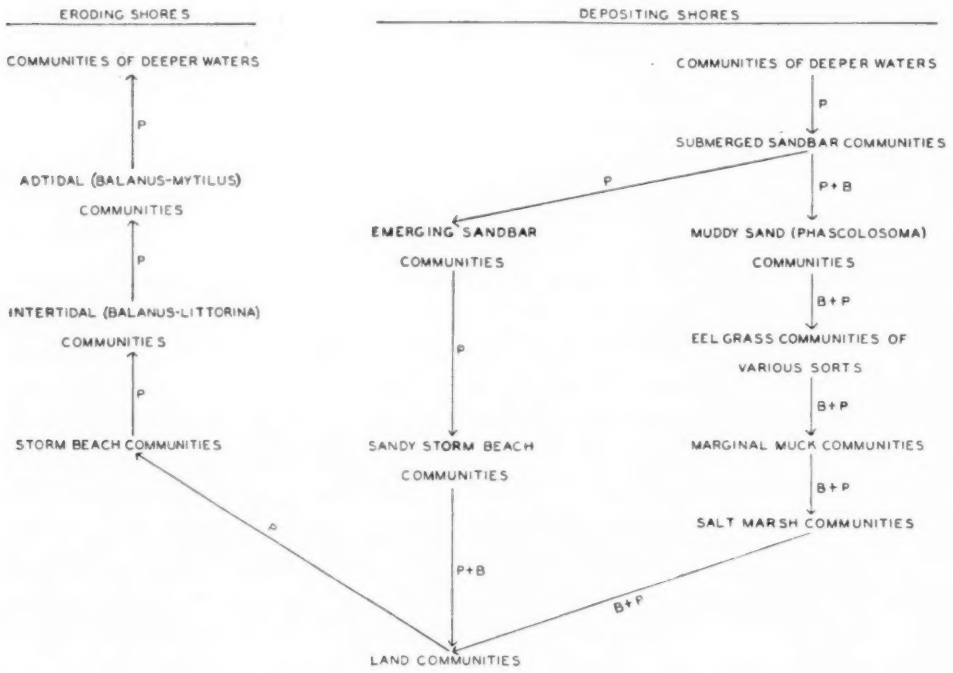
a rake brought in two or three at one pull, I learned to expect none in the rake swaths on either side. Likewise the turbellarian, *Procerodes wheatlandi*, shows differential distribution even in the narrow zonation found on the Vineyard Sound side of Woods Hole. I know of but one locality along this shore line where *Procerodes* may be taken, although there are several places that appear to present similar habitat features. Even in the one strip where they are found, their occurrence is erratic. Not nearly every stone carries its quota; rather they are scattered, isolated, or as is more frequently the case, are collected here and there in small clusters which may contain fifty or more on one stone. Similarly, differential distribution of other animals is to be found on wharf pilings in the same region.

The botanists are not agreed concerning the random nature of plant distribution in a uniform habitat. Gleason (1929) thinks that distribution in accordance with the laws of probability and chance is characteristic of vegetation. Romell (1930) comes to the opposite conclusion. This point has been investigated recently for animals, by Gray and Treloar (1933). To be sure, they used the insects in a uniform stand of alfalfa rather than the animals of the sea bottom. Their methods tended to mask rather than to emphasize heterogeneity of population density, yet this was proven to exist for six of the eleven classifications used in collections from a field of 2.25 acres.

Such differential distribution would be expected if the existence of an animal community is based in part on intrinsic relations rather than wholly on extrinsic forces. The reality of the communities discovered by Petersen is to be accepted the more readily in that the bottom sampler method without special precautions presupposes random rather than differential distributions.

I know of no equally accurate quantitative analyses of submerged marine populations. Neither do I know of an investigation of the relationship that samples taken by the Petersen bottom sampler bear to the realities of distribution. Petersen himself recognized limitations with regard to type of bottom, plant cover, and particularly with regard to active animals. Studies which would serve to evaluate this method accurately could readily be made on tidal flats where there is a relatively large tidal amplitude. Under the conditions furnished by these flats, the efficiency of the method could be established for different depths and the number of samplings necessary to establish distribution within a certain selected tolerance of error. Gray and Treloar, in the study just cited, find that the number of collections necessary to secure a reduction of error to fifty per cent of the "true" value ranges, for the animals studied, from 125 to 1075 individual sweeps of a collecting net, with a mean of 650. From 3100 to 26,975 sweeps of the net in the alfalfa field they investigated, would have been needed to reduce the error to ten per cent of the "true" mean. Even a ten per cent error is too great for quantitative work.

The question of ecological succession in generalized marine communities has been discussed relatively little. Ten years ago (Allee, 1923a) I had the temerity to attempt to arrange the easily recognizable inshore communities near Woods Hole in successional order with respect to the communities of the open water. This arrangement, radically revised for the communities of the eroding shores, is schematically summarized in Figure 1.



Legend

FIG. 1. Schematic diagram of community evolution in the Woods Hole region. Arrows show direction of succession. Letters show the principal forces acting; P, physiographic, B, biotic.

The conditions existing along this coast suggest a titanic struggle between land and water. In this struggle the communities we have been discussing occupy that part of the zone of tension which lies below the high tide mark. The principal forces causing succession are physiographic (P. in Figure 1) rather than biotic (B). In fact, along eroding shores, biotic forces are negligible in effect, and the biotic communities occupy appropriate niches which they have done little or nothing to make available, and hence, in the strictest sense, these are examples of physiographic development of habitat, rather than of biotic succession. The story is partially different for the depositing shores. At the mouth of the Mississippi, for example, much sediment is borne in but near Woods Hole there is an absence of fresh water streams. Even so, the mud which accumulates in back bays free from currents shows only about nine per cent loss on ignition and is mainly not of organic origin.

Along these depositing shores, by leave as it were of physiographic forces, there is an opportunity for the biota to hasten an evolution from the communities occupying clean sand to those of marginal muck, and on through the salt marsh toward the land climax of the region (cf. Shelford and Towler, 1925, p. 70 (Shelford, Weese, *et al* 1934).

There is not time, nor, I fear, are adequate data available, to discuss with assurance the organization of marine communities and the degree of importance of the different constituents. Although important beginnings have been made by Shelford and associates, further light on this set of problems must wait for the development of an adequate evaluation of the quantitative collecting methods now available and perhaps for the development of improved quantitative collecting. It must also wait for the proper combination of adequate quantitative data with expert knowledge of the physiological needs and adjustments of the constituent organisms.

Neither is there time to discuss the interrelation between animal communities of the bottom and those of plankton and nekton of the waters above them. Petersen found a distinct relationship between communities in the substratum and those dwelling on it; on the other hand, he thought the plankton organisms were of little importance for bottom dwellers, but that eel grass was of great importance. This eel grass is not eaten when fresh, but the detritus after decay forms a thin layer on the surface which is used as food. Without exact data available, I am inclined to believe that in the Woods Hole region there is a much closer correlation between the animal communities of the bottom and those of the waters above them than Petersen's studies would indicate.

Further, there is not time to consider the currently much discussed problem of population fluctuation. Jensen (1919) and Blegvad (1928) show that the bottom invertebrates do not have equally good breeding years annually, but, as we know well for fishes, have important year classes which result from favorable breeding conditions. *Abra* has a good year almost biennially; *Solen*, less often; *Mya truncata*, only occasionally. The good year classes of fishes do not seem to be closely correlated to the good year classes of their food organisms and hence must be controlled by other factors, at least to a large extent. Parenthetically, with local exceptions, the production of bottom-dwelling or bottom-feeding fishes in Danish waters does not seem to be directly correlated to the abundance of their food organisms; at least the relationship is not a simple 1:1 ratio. However, there is good evidence, based in part on fisheries statistics (Volterra, 1931); see also Nicholson, (1933) that fluctuations in numbers leading to the cycles of which nowadays we are quite conscious, may result from the interplay of biological forces in a relatively stable environment. In so far as this is true, these cycles emphasize intracommunity relations rather than the effect of impinging physical forces.

And now, having filled my time and a trifle more, in approved symposium style, with materials with which my audience was probably acquainted already, let me summarize in a few words the points I have been trying to make. Doubtless this succinct summarizing statement would have served many present better than the rambling discussion which has preceded it; certainly, for many not present, it will be the only part of the published paper which will be read.

1. The recognition that organisms live in communities which can be treated as superorganismal units is not so recent as many have supposed. Although the major advances in recent years have been initiated by botanists, there is a long and honorable history of the study of marine animal communities and some of the more important of recent advances, especially the recognition of biotic communities rather than communities of either plants or animals taken separately have been more generally supported by animal than by plant workers.

2. Even so, many studies in modern oceanography lack the community approach and especially show a lack of appreciation of advances made as a result of studies on land communities of plants and animals.

3. In regions where the physical factors of the environment sub-divide the marine habitat into relatively small areas, the marine communities appear to be controlled largely by these physical factors.

4. In neighboring regions where environmental conditions are apparently uniform over a greater area, the distribution of marine organisms is not random, but there is evidence of differential distribution caused, at least in part, by the biological interrelationships characteristic of a biocoenose.

5. Even in regions where communities are limited to narrow ranges by physical factors in the environment, careful collecting frequently reveals differential distribution of the animal aggregation type (Allee, 1931, 1934).

6. The picture that finally emerges from this survey of marine coastal communities is of a sort of superorganismic unity not alone between plants and animals to form biotic communities, but also between the biota and the environment. If the biotic community concept deserves the emphasis furnished by the redundant term, bio-ecology, I suppose the concept just given should be designated by the super-redundancy, geo-bio-ecology. Analysis of this complex challenges our best individual and coöperative power. Failure to recognize the essential unity of this animal-plant-environmental relationship retards progress in oceanic studies.

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